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THE BIOLOGY OF SPIDERS

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TRAP-DOOR SPIDER (*Nemesia congener*) IN NEST. × 1.

Frontispiece.]

[*H. Main, photo.*

THE BIOLOGY OF SPIDERS

BY

THEODORE H. SAVORY, M.A.

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"Man wants to know, and when he ceases to do so he is no longer man."

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F. NANSEN

March 1942

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DEDICATED

TO

MY CHILDREN,

WHOSE INTEREST IN THE PROGRESS OF THIS BOOK
IS GRATEFULLY ACKNOWLEDGED TO HAVE
BEEN A VERY REAL ENCOURAGEMENT
TO THEIR AFFECTIONATE
FATHER.

PREFACE

EVERY writer, it has been said, sees in imagination a desert island where he would be free to work undisturbed. I myself periodically visit one such solitude when each year I receive and read the precious blue paper-covered booklet which constitutes the Arachnida section of the Zoological Record. That invaluable annual (how could we get on without it ?) always inspires me to dream of my island, yet shared peradventure with certain other persons, where I should be able to write two books which seem to me to be wanted.

One of these is a complete work on British Spiders—a Blackwall, a Pickard-Cambridge up-to-date. It is, indeed, not impossible that such a book may one day appear.

The second is suggested by the very obvious fact that the papers published on spiders fall into two categories. One consists of faunal lists, reports on collections made by expeditions and descriptions of new species ; the other of records of observations on the structure, habits and behaviour of spiders. It has always seemed to me that the second category ought to be used as material for a synthetic work, dealing with every aspect of spider-study other than systematic diagnosis of families, genera and species. The ideal for such a book would be that its reader should have no need to refer to any other work for information about any topic pertinent to the biology of spiders.

That, at least, is the ideal with which one might set about the writing of such a book as this. In practice it is very difficult to attain, as is common with ideals. When one has

only devoted half of one's life to the study of spiders, there is bound to be much that one has never read, much that one has forgotten, much of which one has never heard of, and it is seldom possible to make the acquaintance of every one of the several hundred papers which one feels that one ought to know. But an effort may be made, and no one who is at all familiar with the literature of spiders will fail to realise how much I owe to the work of my predecessors.

In the nature of things, therefore, such a book as this does not lay claim to complete originality. Much of it is necessarily but an integration of the work of others, previously scattered in several languages all over zoological literature, correlating their results and opinions into one accessible and more or less homogeneous whole. "That is the worst of erudition," says Dr. A. C. Benson, "that the next scholar sucks the few drops of honey that you have accumulated, sets right your blunders and you are superseded. You have handed on the torch, perhaps, and even trimmed it. Your errors, your patient explanations, were a necessary step in the progress of knowledge; but even now the procession has turned the corner and is out of sight." I do not presume to set right or to supersede any of my predecessors and I can but express the hope that they will not regard my borrowings as "the worst of erudition," but as studied compliments to themselves.

At the same time certain interpretations of the behaviour of spiders, much of the earlier parts of Chapter VII and of Chapter IX and the major part of Chapter XV may lay claims to originality as the work of the present writer.

The book owes much to the suggestions and careful reading of Prof. J. Arthur Thomson. I am glad to take this opportunity of expressing my thanks to him for all that he has done.

It gives me very great pleasure to acknowledge the help I have received from my own pupils. Their enthusiasm has not only been an encouragement to myself, but has had practical results which are incorporated in the following pages. I owe Fig. 34 to the dissections of G. T. Pitts and M. L. Meade-King, and Fig. 48 to a dissection made by L. W. Spratt. Fig. 15 was drawn by G. T. Pitts. Help was also given by C. M. Adcock and R. D. McKelvie.

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THE BIOLOGY OF SPIDERS

CHAPTER I

GENERAL CHARACTERISTICS OF THE CLASS ARACHNIDA

AMONG the wonders of Natural History, few things are more remarkable than is the multitude of small many-legged animals, often of beautiful structure, striking habits and complex life-histories, yet seldom obtruding themselves upon our notice. Down among the grass roots, under the drifted leaves and amid the fallen pine-needles lives a Lilliputian populace, fighting and slaying, mating and bringing forth young, pursuing a life vivid, intense and fierce, of which the Brobdingnagian mammal is in most cases quite unaware. Well represented among these small Arthropods are the Arachnids, such as spiders, which form the subject of this volume. Elusive creatures they are, unversed in the arts of self-advertisement, or taught by age-long experience to refrain from testing its doubtful advantages. Save for a few spiders, a scorpion or two, and here and there a mite that has long been unsuccessfully persecuted, mankind neither sees them nor gives them heed. He has paid, and he yet will pay, a heavy price for this neglect, as now he is beginning to discern. It is here our purpose to look more closely at these little creatures, to read in the book of their lives stories more wonderful than the imagination of man has conceived; to find, too, that in their little domain the same principles hold as in our larger world, for

the same laws hold throughout the length and breadth, the height and depth of the continued miracle that we call Life.

The name Arachnida (ἀράχνη, a spider; εἶδος, shape) was created by Lamarck when in 1815 he separated Scorpions, Spiders and Mites from the order Aptera of the Linnean Insecta. The Class Insecta of Linneus was almost co-extensive with the Entoma of Aristotle, as well as with the modern phylum Arthropoda founded by von Sievold and Stannius. The phylum includes an enormous number of segmented Invertebrates, whose most characteristic feature is the specialisation of one or more pairs of the appendages in the vicinity of the mouth into jaw-like structures or gnathites. This specialisation has been accompanied by a shunting backwards of the mouth, which thus comes to have more in front of it than the simple pre-oral lobe or prostomium, familiar in the earthworm and characteristic of all the Annelida. This backward shunting of the mouth implied simultaneously an advance in cephalisation, that is to say, the formation of a definite head from a number of segments, rings or somites which have become pre-oral, the "prosthomeres" of Lankester. Among the Arthropoda, three different types of head are recognisable, according to the number of prosthomeres which go to its composition. Peripatus, a primitive type of Arthropod, has but a single pre-oral segment. The Arachnida represent a stage of progress intermediate between *Peripatus* and the Crustacea or the Insecta in that they have two prosthomeres, while both Crustaceans and Insects possess three. This gives us some idea of the position of the Arachnida in relation to the other Arthropod classes. The gnathites which are accessory to the Arachnid mouth are borne by the third somite; these animals are describable as tritognathous, *Peripatus* being deuterognathous and the Crustacea and Insecta tetartognathous.

The diprosthomerous condition of the Arachnida is seen only in the adult. In the embryo the second somite and its appendages are not yet actually in front of the mouth (Fig. 1). The existence of two prosthomeres is indicated

both by their coelomic cavities and by two nerve-masses or neuromeres. Appendages do not exist on the first somite, though it is possible that they are represented by the eyes. The chelicerae are the appendages of the second somite. The five conspicuous limbs which follow, namely, the palps and the four pairs of legs, indicate a coalescence of five further somites, the result being the construction of a cephalothorax, *i.e.* a head or cephalon and breast or thorax fused together. The reason for being patient with technical terms like " prosthomeres " is that they are less misleading

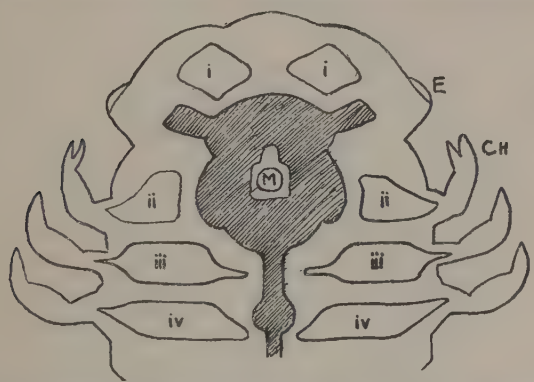


FIG. 1.—Diagram of Embryo Arachnid Head. In embryo, somite ii is not yet in front of mouth. From Lankester. E, eye ; CH, chelicerae ; M, mouth ; i–iv, coelom of somites, 1–4.

than easy-going popular words like " head " and even " thorax," which are too suggestive of man or mammal.

The region behind the cephalothorax, the opisthosoma, generally called the abdomen, is composed of twelve segments or somites. The first of these is the so-called pregenital segment of scorpions and is represented by the " waist " of the spider. The second and third somites of at least some of the terrestrial forms bear the lung-books. The fourth and fifth somites are of interest because in spiders they retain their appendages in the form of spinnerets, of which primitively there are eight, four (two endopodites and two exopodites) to each segment. The last seven somites are devoid of appendages in all living forms. The

last may carry a post-anal telson, represented by the spine of the King-Crab, *Limulus*, and by the sting of the scorpion.

The alimentary canal of Arachnida has the stomodeal and proctodeal invaginations of the external chitin possessed by most Arthropoda. It is a more or less straight tube, provided as a rule with blind glandular outgrowths from the mesenteron which increase its absorbtive action. Excretory Malpighian tubes discharge waste products into the hinder part of the canal in all the terrestrial forms. True nephridia are not found in Arachnida; other ducts from the body-cavity to the exterior are represented by gonoducts and by coxal glands. The latter are the only excretory organs of *Limulus* and are found in other Arachnida also.

The blood system is of the lacunar type common to Arthropoda. The heart, a simple tube with valved ostia, is situated dorsally in the opisthosoma. The arteries are better defined than the veins, which tend to expand into sinuses. The blood is colourless and contains numerous corpuscles.

Respiration is effected by three different methods. The marine Merostomata breathe by gills, which are borne externally as appendages of the segments of the opisthosoma. In the terrestrial forms these are replaced by lung-books, within the body, but still to be regarded as appendages, extremely modified. In addition, respiratory tracheae are also found, and may co-exist with lung-books or may altogether replace them.

The "brain" is a supra-oesophageal ganglion which supplies the two prosthomeres: the posterior ganglia are more or less fused so that five separate ganglia are never found in the prosoma of the adult. Of the sense organs, two are predominant, the eyes and the organs of touch. The eyes are simple and of the characteristic Arthropod type, never more than eight in number. Several blind forms are known. The sense of touch is acutely developed in connection with an elaborate system of complex sensory hairs. Some of these hairs probably function as auditory organs.

Asexual reproduction is unknown in Arachnida and parthenogenesis is extremely rare. The sexes are separate although gynandrous forms are sometimes found as freaks. Sexual dimorphism is not great and may be totally lacking as far as external appearance is concerned. In spiders, however, the male is distinguishable by its smaller size and by the modification of its palpi into sexual organs. Both viviparous and oviparous forms are found. Development of the young is usually direct, but metamorphosis occurs among the Mites.

Arachnida are generally carnivorous and attack and eat living prey, but some will eat dead flesh and among the Mites the diet is more varied. Mites alone include parasitic forms, the hosts attacked being both animals and plants. Few examples of organised communal or society life are known ; activities are solitary and generally nocturnal.

The habit of producing quantities of silk and of spinning this either into a snare for prey or into a protective cocoon for eggs is one of the most striking peculiarities of the Arachnida, inasmuch as, though a thoroughly successful device, it is almost unknown outside this Class.

The Arachnida as a group provide an interesting comparison with the Crustacea. Whereas the numerous living and fossil members of the Crustacean class give us good evidence of its racial history from primitive to specialised forms, the primitive Arachnida are not so readily discernible. Limulus and the scorpions, the nearest living approach to such creatures, are not primitive animals in the biological sense and the many small and simplified Arachnida alive to-day are degenerate types, and not survivals of an early ancestor.

Sir Ray Lankester has suggested a solution of the problem by the following argument. If we may expect a reasonable parallelism between the Crustacea and the Arachnida, then we must be prepared to find differences between the scorpions and the primitive Arachnida at least as great as and probably comparable to the differences between a higher Crustacean such as a crab and a primitive one like *Apus*.

The higher Crustacea, like the higher Arachnida, are characterised both by a definite typical number of segments to the body and by an obvious grouping of these segments into divisions or tagmata. The lower Crustacea have a very variable number of segments and they show less inclination to group these segments into sharply defined regions. We are therefore led to expect of the primitive Arachnida less exactitude of segments in respect of both numbers and arrangement. With these considerations in mind, Lankester has pointed out that it is not unreasonable to regard the Trilobites as representatives of the distant past of Arachnid history. They are monoprosthomerous, which differentiates them from living Crustacea: they have lateral eyes which resemble nothing so closely as the lateral eyes of *Limulus*, and a superficially similar trilobation of head and body is seen in the larva of *Limulus*. There are other features in the structure of these interesting fossils which seem to confirm them in such a position. For instance, they show a varying tendency to unite the posterior segments into a pygidial shield comparable to the metasomatic carapace of *Limulus*, and some of them carry a large posterior spine like that of scorpions. Some other zoologists, however, maintain that the Trilobites are really more nearly allied to the Crustacea and they will not, in this book, be considered as members of the Arachnida. Primitive Arachnida may have been similar in structure and habits to *Limulus*; or we may seek to conceal our ignorance by saying that the relation between the primitive Arachnida and *Limulus* is comparable to that between the Trilobites and the lower living Crustacea.

The Arachnida are, then, taken to be a class of eleven orders, one of which is represented only by fossil forms. The classification is as follows:

Class **ARACHNIDA**

Sub-class **DELOBRANCHIATA** (= Merostomata)

Arachnida with exposed gills, breathing dissolved oxygen.

Order XIPHOSURA

Marine Arachnida with prosoma of horseshoe-like outline ; opisthosoma unsegmented ; telson in the form of a spine.

Order EURYPTERIDA (=Gigantostraca)

Fossil Arachnida, nearly all marine, found in Palaeozoic formations.

Sub-class **EMBOLOBRANCHIATA**

Arachnida with lung-books or tracheae or both, breathing free oxygen.

Order SCORPIONIDEA

Segmented Arachnida with chelate chelicerae and palpi ; opisthosoma divided into a mesosoma and a tail-like metasoma, each of six segments ; telson in the form of a sting ; four pairs of lung-books ; a pair of pectines on the second mesosomatic segment.

Order PEDIPALPI

Arachnida with two-jointed non-chelate chelicerae and strong palpi ; first pair of legs used as tactile organs ; the prosoma unsegmented, the opisthosoma segmented ; one pair of lung-books.

Order ARANEAE (= Araneida)

Arachnida with two-jointed non-chelate chelicerae carrying the orifice of a poison duct ; palpus of male bears a sexual organ ; the prosoma always, the opisthosoma usually unsegmented ; the appendages of the latter function as spinnerets ; respiration by both lung-books and tracheae.

Order PALPIGRADI (= Microthelyphonida)

Arachnida with three-jointed chelate chelicerae ; prosoma consisting of an anterior portion unsegmented, and a

posterior portion of two segments; opisthosoma of eleven segments, bearing a flagellum of fifteen joints.

Order SOLIFUGAE (= Solpugae)

Arachnida with two-jointed chelate chelicerae and sensory palpi; prosoma has the last three segments free; opisthosoma segmented.

Order CHERNETIDEA (= Pseudoscorpiones)

Arachnida with chelate chelicerae, bearing the opening of the spinning organ; palpi large and chelate; opisthosoma segmented; respiration by tracheae.

Order PODOGONA (= Ricinulei)

Arachnida with prehensile palpi; tarsus of third leg of male bears a sexual organ; respiration by tracheae.

Order OPILIONES (= Phalangidea)

Arachnida with three-jointed chelate chelicerae; prosoma contains odoriferous glands; opisthosoma segmented; no spinning organ; respiration by tracheae.

Order ACARINA (= Acari)

Arachnida with suctorial and biting or piercing mouth-parts; opisthosoma nearly always segmented; respiration by tracheae; life-history includes metamorphosis.

The fifth of these orders, that of the spiders, is the one with which the bulk of this book is concerned, and it may be as well at this point to clear up the unfortunate uncertainty as to how it may best be named.

C. Clerck, who wrote a book on Swedish spiders, "Svenska Spindlar," in 1757, used *Araneus* as Linneus had done for every spider, recognising no generic divisions. Subdivisions were first made by Latreille in 1804, when he

used *Araneus* for the common garden spider, *Epeira diademata*. At the same time he suggested Araneides as a family name and Leach changed this in 1817 to Araneidea. Araneida was a form subsequently used solely for the sake of uniformity with the names of other arachnid orders. However, in 1827 Latreille, somewhat casually, transferred *Araneus* to the house spider, *Tegenaria domestica*, whereon Walckenaer, realising the disadvantages attaching to the name as a generic term, set up *Epeira* and restored *Tegenaria*. With the disappearance of *Araneus*, Araneida, which signifies "like the genus *Araneus*," became meaningless, and Sundevall, in 1833, proposed Araneae, to which there is no such objection.

The final complication was due to the revival by Simon in the first volume of his *Histoirie Naturelle des Araignées*, of *Araneus* as an immense genus, embracing *Epeira* and many of its allies. His subdivision of the genus into several artificial groups was no more satisfactory than the older system of separate genera, with the result that most authors have not followed him and *Araneus* has not gained general acceptance. In the form *Aranea* it is used in America, but on the whole it seems wisest to use Araneae as the name of the order.

It is not too much to say that of the eleven Arachnid orders, spiders are the dominant group, dominant both by virtue of their numbers and their world-wide distribution. Mites alone seriously challenge them in these respects; all the others are limited in range and inconspicuous in activities.

In taking a view of the order of spiders as a whole it is soon clear that they stand for several reasons detached from all other groups.

The first feature of this isolation is their copious use of silk. Some insect larvae and some of the other Arachnida can produce silk, but other spinners make of it only an occasional or a particular use, whereas the whole of the spiders' life shows an entire dependence on this invaluable material. "The young spider is born into a silk nursery,

and on a silk monoplane it flies away; with a silk web it catches its food, binding up with silk threads and ribbons its struggling prey or its bitter enemies. It drops from peril on a silk rope, of a silk sheet it makes its cocoon, its eggs wrapped round with silk cushions. In a silk chamber the old spider sleeps through the cold of winter, and even in death it is sometimes wrapped in a silk shroud." So complete a reliance on a single material is altogether unique.

Secondly, the spider is alone or nearly alone in spinning a web or snare for its prey. Few of us, coming by chance upon a spider's web, realise this aspect of its nature. Birds build nests, beavers dams, bees combs, termites cities, but the spider builds a trap. The only other instance of such a structure is the web made by the larva of the caddis *Hydropsyche*.

Thirdly, spiders have an anatomical peculiarity which it is hard to match elsewhere in the animal kingdom. The palpi of the mature male become modified at the final moult into complex intromittent organs, but they have no direct connection with either the testes or the vasa deferentia. The spermatozoa produced by these organs, which are situated in the abdomen, must therefore be transferred to the palpi before they can be passed in mating to the female. This picking up of the semen by the palpi (the "sperm-induction," as it is called) is one of the spider's most extraordinary actions, and incidentally one of the hardest to witness. Such a separation of testis and penis is all but unheard-of—one had almost said impossible.

That a group of animals should possess three peculiarities like these is not a little remarkable, and no one would be surprised if they were among the most popular subjects for study by zoologists throughout the world. And yet the striking fact is their neglect by naturalists in all times and countries. It is not as though spiders were rare or few in kind or difficult to catch, for they are none of these, and long before we have become aware of the peculiarities described above, they have advertised themselves, thrust themselves

upon our notice with their orb-webs—one of the most wonderful structures in the animal world.

It seems possible that the spider's very isolation is partly responsible for their neglect. The spider does not illustrate, better than any other "type," any principle of zoology, except, perhaps, evolution; and the spider's contribution to the evolution theory (see Chapter XV) is of very recent recognition. Thus the spider is immediately relegated, or shall we say promoted, from the domain of the student to that of the specialist. This is the more understandable because it is a very difficult animal to dissect, and under the scalpel of the inexperienced generally becomes a most lamentable-looking object.

Again, modern zoology is almost wholly organised in terms of evolution, and the spider's isolation places it in an evolutionary backwater which, successful though it may have been, takes it out of the main stream of past history. The phylogenist can pass it by unheeded and suffer nothing for his neglect.

Lastly, the spider has no economic importance. It does not attack the food, the clothing, or the houses of man; a few attempts to use its silk have been pathetic disappointments; and its occasional captures of noxious insects are counterbalanced by its catholic taste and readiness to eat without discrimination man's entomological allies.

When one leaves the ranks of zoologists for inquiry among other persons, one finds not neglect so much as active dislike, and this too is not a little remarkable. Such an attitude towards the spider seems to be a universal human trait, more widely spread than claustrophobia, and much more difficult to explain. A natural dislike by a careful housewife of a creature whose propensity for filling her rooms with cobwebs adds to her work, is understandable, but in a different category altogether is the intensity of the feelings from which some people suffer. Every one of us must have many such persons among our acquaintances. In other respects, these people may be not only normal, but even admirable—giants among men. An instance that comes

readily to the mind is that of H. R. Bowers, who, had he not been involved in Captain Scott's disaster, would undoubtedly have become one of the greatest polar explorers of the age, and who yet had such an aversion from spiders as to describe them as more loathsome than even the land-crabs of South Trinidad.

Psychologists might be able to discover the origin of such phobia in an occasion of childish fright. It is undeniable that no creature is more likely than a house spider to appear unexpectedly, and, with its straggling legs and unusual mien, to give a shock to a child. Were this shock to be repeated, as well it might be, the ultimate result in the adult mentality might be the " instinctive " horror which is so common.

It is this attitude of mind which prompts two of the questions which so frequently recur in casual conversation—" What is the good of studying spiders ? " and " What is the use of spiders ? " Both questions, though generally put without any intention other than sheer banality, implicate fundamentals of biology, and are well worth answering at the beginning of such a book as this.

The first question betrays ignorance of the spirit of research and a lack of sympathy with the whole outlook of the scientific mind. Scientific studies are not carried out because of the use to which men may ultimately be able to put their results, and the existence or otherwise of any such " practical application " (abhorrent phrase !) is not a reason either for their prosecution or abandonment. There is a close parallel in point of view between pure biological research and polar exploration, and Nansen could exclaim in surprise, " People perhaps still exist who believe it is of no importance to explore the unknown polar regions." He ends this well-known passage with words which ought to be inscribed in every laboratory, " The history of the human race is a continual struggle from darkness towards light. It is therefore to no purpose to discuss the use of knowledge ; man wants to know, and when he ceases to do so he is no longer man." The scientist, like the polar explorer, works because

man wants to know, because both are looking forward to the distant day when all shall be known. When that day may come, what that knowledge may mean, he cannot hope more than dimly to foresee. But it is his faith.

The second question is, if anything, more futile. It presupposes, first, a purpose for the universe as a whole, and, secondly, that this purpose is closely connected with the well-being of Man ; whereas what is actually known is that the facts of biology seem to arrange themselves in an ordered plan. That we can thus think out the universe and, however painfully, arrange it in a definite plan of events that lead to one another and tend somewhere, though we know not where, may be taken as showing that there is purpose behind it all. But this is an altogether different matter from the assumption that every form of life was created to be of direct use to man. The use (so-called) of the spider or of any other creature is that it is a cog in a wheel of this vast machine. As such it gives things in general an impulse in some direction. No one knows enough to say whither, but certain it is that the economy of Nature would be different without it.

A part of this greater purpose, and one which is more the concern of the naturalist and less that of the philosopher, is the evident purposiveness in the activities of every animal. All that it does tends in one direction—to preserve and increase it and its kind. This is the real distinction between all that is living and all that is not, this quality which must have been present in the primaeval living matter, though how it arose and to what it is due no man can say. In this book we have to consider first the structure of the spider as adapted to its various actions, and then to pass to an account of the habits themselves. We can best appreciate the latter, when we understand the part played by the spider in the scheme of things.

CHAPTER II

THE EXTERNAL STRUCTURE OF SPIDERS

In Biology, as in other branches of Science, observation of facts provides the basis on which all subsequent progress depends. The discovery of the structure of animals' bodies is one manifestly important aspect of these preliminaries, but it is well to recognise that it is only a part of the problems of biology and to realise clearly the position occupied by morphology in the wider science.

The progress of Science is an orderly march by recognised steps, constituting a process generally described as "scientific method." The procedure has been outlined in a familiar passage by de Morgan. "Modern discoveries," he wrote, "have not been made by large collection of facts with subsequent discussion, separation and resulting deduction of a truth thus rendered perceptible. A few facts have suggested a hypothesis, which means a supposition, proper to explain them. The necessary results of this hypothesis are worked out, and then, and not till then, other facts are examined to see if their ulterior results are found in Nature."

The stating of the hypothesis is a process of inductive reasoning, a passing from the particular to the universal. This is followed by the reverse process of deductive reasoning, or passing from the universal to the particular, while the ultimate test by actual experiment is the most characteristic feature of the Newtonian or modern scientific method. It is clear that in this process the greatest risk is attached to the induction, a risk which was embodied in the late Lord Rayleigh's oxymoron, "Never base your theories upon facts, for if the facts are disproved, what

becomes of the theory?" So great, indeed, is this risk that it is often assumed, in popular speech, that to argue from the particular to the general must necessarily be fallacious. That it is not so, a moment's reflection will prove.

It is now to be emphasised that the Newtonian method is not invariably applicable to every branch of science. The method depends on the material, and every student knows that the Newtonian method is best illustrated by examples from Physics. Biology must as yet rely very largely upon more empirical methods and this is especially true of morphology. Experimental treatment is possible and frequent in dealing with problems of physiology, but morphology has scarcely passed the stage of observation followed by inductive inference. Hence the necessity for clearness in comprehension of the facts of anatomy and for frequent checking of observations by comparisons. "Comparative Anatomy" has long been the name of a branch of zoology, while comparative physiology is far less familiar.

These considerations introduce us to one aspect of the study of morphology, but another is no less essential. Structure and habits are not unrelated, but are mutually dependent portions of a whole which is the adaptation of the organism to its environment. Looked at from this point of view the facts of morphology become living realities; they come alive. It is often clear enough that morphological facts cannot be understood unless the functions of which different structures subserve be kept steadily in view. Often the function is obvious, but in the morphology of the Arachnida there must also be included a number of facts of which the functional importance is at present by no means so obvious. It is, however, unwise to neglect them for this reason, since advances in our knowledge may well depend upon our remembering them. Such an outlook gives to the whole subject of the anatomy of spiders an intense interest. Spiders are a highly specialised group, with powerful organs and efficient methods, very well adapted to their conditions of living. The uniformity, shown as a general rule throughout the order, is, as it were, emphasised by the

existence of a proportion of truly remarkable aberrant forms, possessing peculiarities, now of this part, now of that. It is specialisation which is responsible for the apparently technical nature of the descriptions of structure in both this and the following chapter: for there is no non-technical way of describing parts which do not exist at all in more familiar animals.

The Cephalothorax

The forepart of the spider's body has in the previous chapter been termed the prosoma. The whole of the literature of spiders, however, uses the word cephalothorax, to which objection has been taken on the ground that it is applied, in different orders, to parts not necessarily the same in origin; for instance, the cephalothorax of the Crustacea includes the first thirteen segments of the body. The same is true of the opisthoma, which is universally called the abdomen, and both terms are now too well established to be altered.

The cephalothorax (Fig. 2) is a comparatively uniform structure. The shield or carapace which bounds it above is occasionally a smooth, regular convex surface, but more often a visible groove divides an apparent head from the thorax behind it. Upon this thoracic region there are generally indentations—a "median fovea" and eight "radial striae" pointing towards the legs. These depressions mark the internal attachments of the muscles of the sucking stomach and of the legs; they are often deeper in colour than the surrounding shield and may form the only pattern borne by the cephalothorax. Sometimes, how-

Fig. 2.—A Spider's Cephalothorax.

ever, dark longitudinal streaks are present; indeed, in many families there is a more or less standard pattern to which its members conform. Again, in some species the cephalothorax is surrounded by spines.

The ocular region is sometimes darker than the rest, and the separate name of clypeus is usually given to that part of the cephalothorax between its extreme fore-edge and the first row of eyes. This clypeus is never present as a definite and distinct part, but its width and its inclination

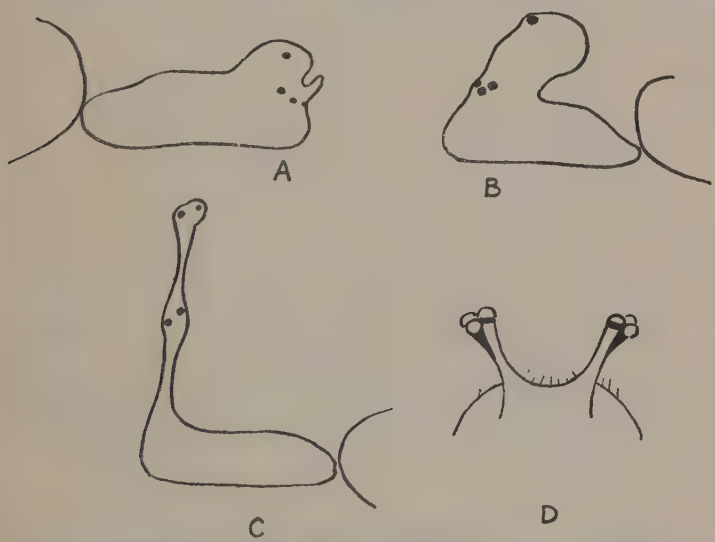


FIG. 3.—Spiders' Eyes. A, Entelecara acuminata. B, Peponocranium ludicrum. C, Walckenaera acuminata. D, Pholcus podophthalmus.

differ and these diversities may be of use in classifying some of the genera of spiders. Occasionally an elevation of the ocular region carries the eyes or some of them in a prominent position, and when this is exaggerated, it produces a remarkable aspect in profile. Some of these are shown in Fig. 3.

THE PEDICLE

The cephalothorax and abdomen are joined by the characteristically slender waist or pedicle, hidden as a rule

by the overhanging abdomen. This delicate junction is protected and strengthened by chitinous plates above and below, known as the lorum and plagula respectively. The shapes of both lorum and plagula are numerous, but there seems to be no principle governing the diversities which are to be found in different families. The lorum is often composed of two pieces, which fit closely to one another, but the plagula is always undivided (Fig. 4).

This pedicle is worthy of more admiration than it generally receives. Even in large spiders its diameter is not

FIG. 4.—A, Lorum of Argyroneta aquatica. B, Plagula of Dysdera cambridgii.

great and in smaller species and their young it must be indeed minute. Yet through it there passes an artery, the nerve cord and a part of the gut.

THE ABDOMEN

The normal abdomen is a more or less elongated cylindrical sac, devoid of all traces of segmentation and very often with no pattern. The greatest possible diversity is, however, found. Pattern and often beauty of colouring and design are conspicuous in many families, and where a pattern or marking of any sort exists, three general features may usually be recognised. Most frequently a longitudinal narrow dorsal mark is present, lying above the heart within and perhaps due to its proximity. In other families, especially the orb-spinners, a broader leaf-shaped mark is found, and is called the folium. Thirdly, small depressed

points, hardened within, and due, like the striations of the cephalothorax, to internal muscle attachments, are often visible symmetrically arranged, and are seen most easily on spiders without other markings (Fig. 5).

Segmentation is persistent in the sub-order Liphistiomorphae. These spiders have several chitinous plates

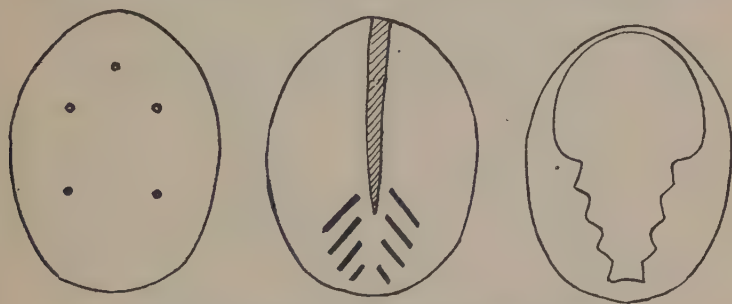


FIG. 5.—Common Types of Abdominal Pattern.

protecting the abdomen both above and below (Fig. 99). This persistence of the primitive condition is unknown in the other sub-orders, save where less perfect traces of segmented ancestry are found in isolated genera. The best example of this is the genus *Tetrablemma* found in

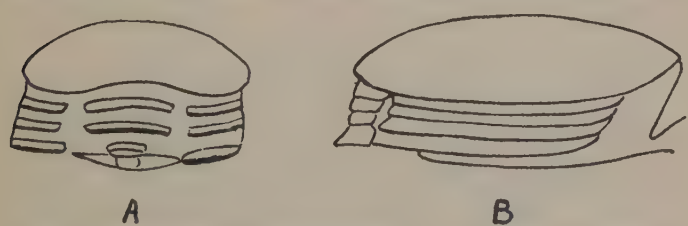


FIG. 6.—Abdomen of Tetrablemma. A, View from behind. B, Profile.

Ceylon. The abdomen of this spider is covered above by a hardened plate, and below two such plates cover most of the surface. In addition, hard folds of cuticle protect the sides and the posterior end of the abdomen (Fig. 6).

An unsegmented dorsal plate of chitin is also found protecting the abdomen in many spiders belonging to the

family Oonopidae. It is probable that this plate is a relic of the earlier segmented terga, which, however, has lost its metamerism.

The diversities in abdominal shape are extraordinary.

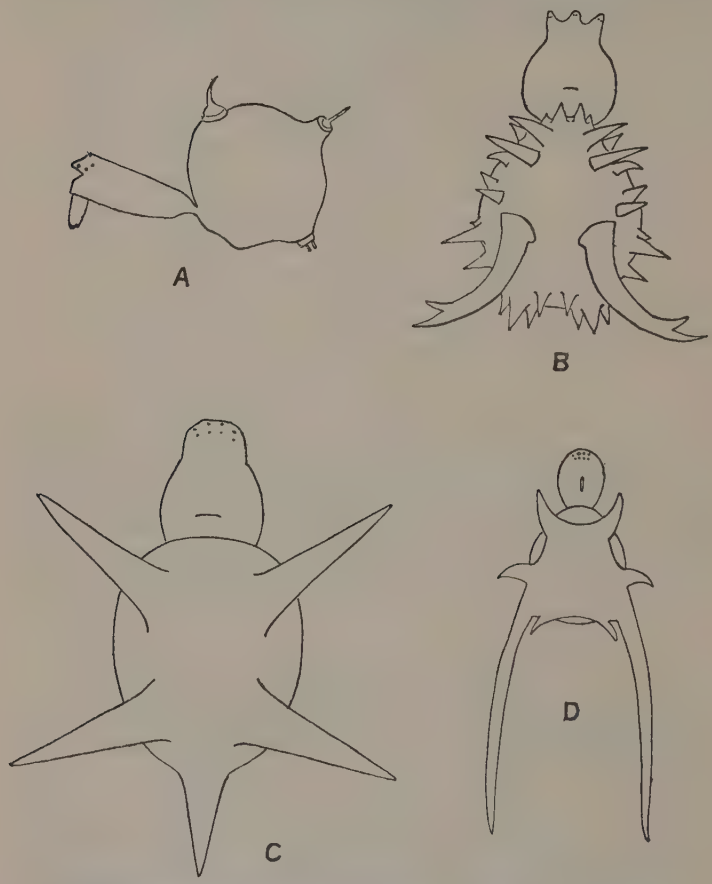


FIG. 7.—Spiders with Spiked Abdomens. A, Phoroncidia trispinosa. B, Pycnacantha tribulus. C, Araneus pentacantha. D, Micrathena cyaneospina.

No cartoonist, trying to draw an absurdly impossible spider, could succeed in achieving a design more bizarre, more fantastically improbable than some of the forms that meet

one's eye as one turns the pages of a collection of papers descriptive of exotic Araneae. These caprices of Evolution may be grouped as follows :—

(1) Forms which protectively resemble objects in their neighbourhood.

(2) Forms which mimic the shapes of other animals.

(3) Forms which are armoured with spikes.

(4) Forms which seem to have neither rhyme nor reason.

The first two groups are described in Chapter VIII ;

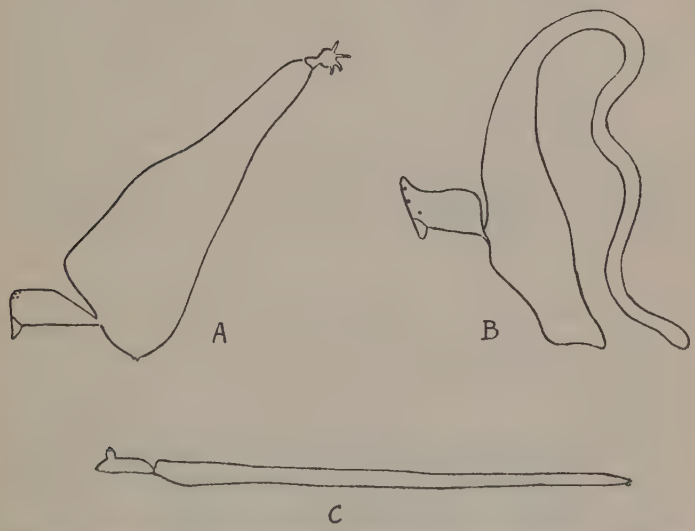


FIG. 8.—Remarkable Shapes. A, Phricotelus stelliger. B, Poltys ideae. C, Leptopholcus signifer.

some specimens of groups (3) and (4) are shown in Figs. 7 and 8. It may be supposed that the shapes shown in Fig. 7 act as a discouragement to such of the hungry as have tender mouths ; but the biological significance of the last group is harder to fathom. It might become apparent to competent observers. It is, however, unfortunately true that much of our knowledge of exotic spiders is limited to descriptions of the structure of dead specimens, received by authorities at home from collectors abroad. Observations of the habits of the animals have been all too rare.

The underside of the abdomen (Fig. 9) shows more features than the upper. The part next to the pedicle is often more convex than the rest and is called the epigastrium. It is visibly separated from the rest by a groove, the epigastric furrow.

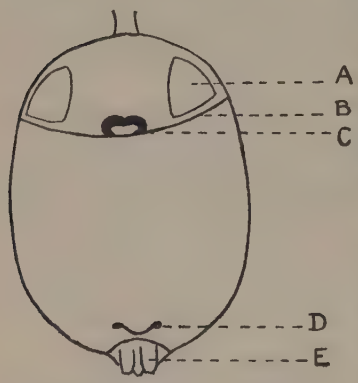


FIG. 9.—Underside of Abdomen. A, Lung-book; B, Epigastric furrow; C, Epigyne; D, Tracheae; E, Spinnerets.

The two lung-books, or the two anterior lung-books of the four-lunged spiders, lie in the epigastric region and are conspicuous as paler-coloured patches. The reproductive organs open between them in the middle of the epigastric furrow.

THE REPRODUCTIVE ORIFICES

The vas deferens of male spiders has but a tiny median orifice, very difficult to discern and unprotected by any epiandrium. The oviduct of the female has, however, a larger aperture, in close association with the single or paired openings of the spermathecae which receive and store the spermatophores of the male, the whole surrounded by and forming part of a complex epigynum. This epigynum shows great diversity in form and in external appearance, so that it becomes the surest, and often indeed the only, way of identifying the female of many species of spiders.

In its simplest form the epigynum is merely a transverse aperture, but this very primitive type is not common. More frequently an opercular plaque, the scape, surrounds and protects the actual vulva, and of such a type three different degrees of complexity may be recognised. In the first of these there are but two simple apertures on the scape, each leading to a spermatheca. An example of this is shown in Fig. 10. The spermathecal openings, however, may be in a

hollow or depression in the scape surface, this hollow being divided by a longitudinal ridge, the guide, Fig. 10. Lastly, the posterior end of the guide may be so broad that its end conceals the openings of the spermothecae altogether. Sometimes this broadening is so great that one may speak

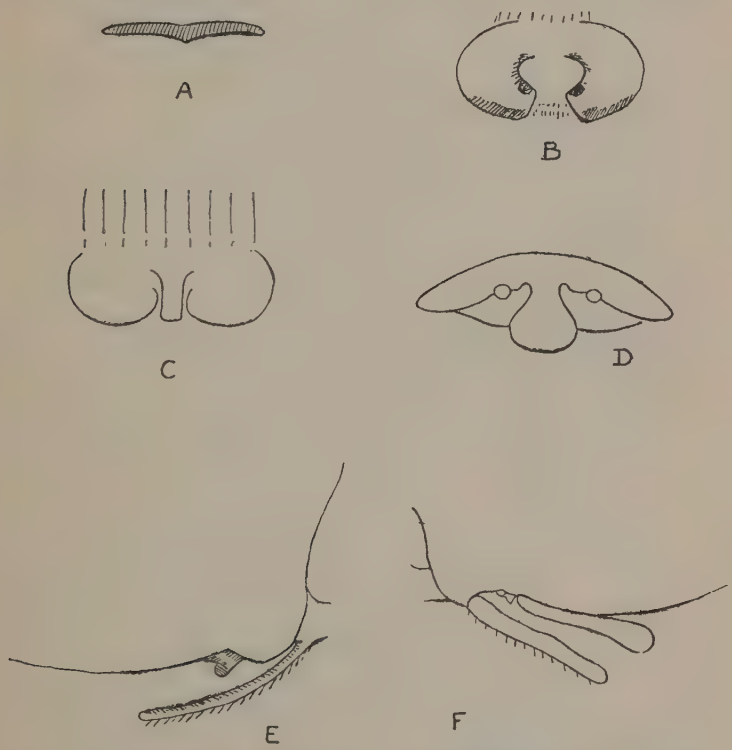


FIG. 10.—Types of Epigyne. A, Liphistus desultor. B, Pirata piraticus. C, Tibellus maritimus. D, Micryphantes rurestris. E, Bathyphantes concolor. F, Bathyphantes nigrinus. E and F in profile.

of the alae of the guide as being these lateral parts under which the spermathecae are to be found.

A more elaborate type of epigynum has a downward projection from the anterior side of the scape. This is called the crochet or clavus ; in appearance it often resembles an elephant's trunk in miniature. The function of this

addition is obscure, for it can scarcely be of much use as an ovipositor: it may play a part in copulation. Its end is usually hollow. Still a further elaboration is found when the crochet is accompanied by another projection, the parmula, from the posterior edge of the scape. These two are in close contact and their opposing faces are hollowed. They form therefore a short tube which acts as an ovipositor.

In many spiders, but not in the Mygalomorphae, nor in those which possess a cribellum, nor in the Drassidae, a small pointed appendage is to be seen just in front of the spinnerets. This is the colulus. It is probably without any function, being merely derived, as was first suggested by Menge, from the more primitive cribellum.

Behind the spinnerets a small tubercle, not always very obvious, carries the anus at its tip. This is sometimes called the anal tubercle, sometimes the post-abdomen. It is relatively more conspicuous in the embryo than in the adult, for it is a vestigial structure representing all that remains of the last seven of the twelve original abdominal segments.

Fig. 11.—A Spider's Sternum. L, Lip; M, Maxillary lobe of palp; P, Pedicle; i–iv Coxae of legs i–iv.

The Sternum

The underside of the prosoma is formed by two unequal plates of chitin named the sternum and labium or lip (Fig. 11). The former is oval or heart-shaped, slightly convex and as a rule marked on each side by four shallow bays or acetabula, opposite the coxae of the legs. Like the carapace, the sternum represents a number of fused segmental plates, and in one sub-family, the Miagrammopinae, a suggestion of this condition is retained, for the sternum consists not of one but of two triangular plates. Since in the Liphistiomorphae the sternum is

uniformly continuous, this condition in the Miagrammopinae may well be a secondary acquisition and not a primitive survival. In many spiders there is a small posterior sternite between the coxae of the fourth pair of legs, possibly reminiscent of a bygone segment and similar to the labium in front.

The labium is sometimes fused altogether to the sternum, but as a rule it is joined to it by softer membrane. Its very variable shape is used frequently in classification—it may be square or elongated, semicircular or oval. Just as the sternum lies between the coxae of the legs so the lip lies between the coxae or the maxillary lobes of the palpi. It forms indeed the floor of the mouth and is generally described as one of the mouth-parts.

The Chelicerae

The appendages of the cephalothorax are the chelicerae, the palpi and the legs.

The chelicerae (chelae, mandibles or falces) are the spiders' very efficient weapons (Fig. 12). Here it may be noted that the number of alternative names for almost every organ is a characteristic of descriptive anatomy in spiders. The cause is the habit of the nineteenth century arachnologists who one after another invented their own terms, in ignorance or neglect of the proposals of their forerunners. Nor has the process ceased yet!

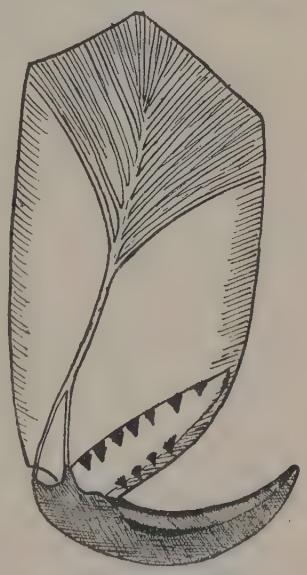


Fig. 12.—A Spider's Chelicera, showing upper and lower rows of teeth, and grooved fang, with strong muscles.

The chelicerae are homologous with the second antennae of Crustacea and not with the mandibles of insects. They consist invariably of two joints, the proximal one being named

the paturon or tige, and the distal the unguis, crochet or fang. In Mygalomorphae, they project horizontally forwards, and strike downwards in parallel directions; in all other spiders they are articulated almost vertically and strike transversely so that the ungues tend to meet in the transfixed prey. Their two parts, though of simple structure, present a very considerable degree of variation in the different forms.

The paturon is a more or less conically shaped joint, generally coated with a few hairs, sometimes, as in *Segestria*, with metallic-looking coloured scales. In some families there is a smooth prominence articulated with the upper end on the outside and called the lateral condyle. This is something of a mystery, but it may be the vestigial exopodite of the primitive biramous pleiopod, the endopodite being the functional portion. The outside of the lower edge of the paturon is furnished with stout teeth, forming a digging organ in those families which have acquired a burrowing habit. This is called the rake or rastellus of the chelicerae. The inner side of the distal end is grooved with a furrow into which the unguis fits when at rest and the two borders of this furrow are denoted as outer and inner in Mygalomorphae, as superior and inferior in other spiders. The superior border may be armed with a brush of hairs or with chitinous teeth. The inferior border is either toothed or altogether unarmed, and this variation in the dentition of the two borders is often a feature of great value in classification. The inner edge of the paturon is usually plain, but in a few spiders it bears a small nipple-like tuber, called the mastidion. This organ is another mystery, its function being difficult to guess. The outer side of the paturon is in some spiders corrugated with a series of ridges which form a stridulating organ, discussed in a later chapter.

In the angle between the paturon and unguis there is a tiny plate or sclerite of chitin called the articular sclerite, and representing, perhaps, an intermediate segment of the chelicerae.

The unguis is nearly always a plain sickle-shaped joint

of very hard chitin, sharply pointed, but it has an unusual shape in *Laches*, and in a comparatively common British genus, *Ceratinella*. The concave edge is grooved and the lower or posterior edge of the groove is usually finely toothed. Near the tip is the orifice of the duct of the poison gland, in a protected position which prevents it from being closed as the spider drives its fangs through its prey.

Some interesting divergences from the typical form of the chelicerae exist. In the common British spider, *Pholcus*, whose chelicerae are small and weak, a projection from the end of the paturon almost meets the unguis, so that the organ is practically "chelate" (Fig. 13). The very remarkable spiders of the family Archaeidae have long and conspicuous cheliderae, and in *Landana* they project downwards in a remarkable manner (Fig. 14). The chelicerae of many ant-mimics project forwards, and carry black spots which imitate the eyes of the ant.

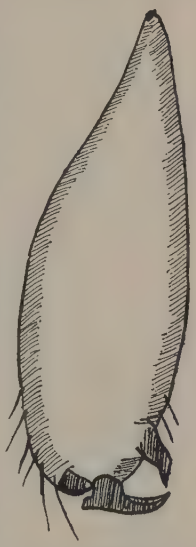


FIG. 13.—Chelicera of Pholcus phalangioides, showing characteristic "chelate" arrangement.

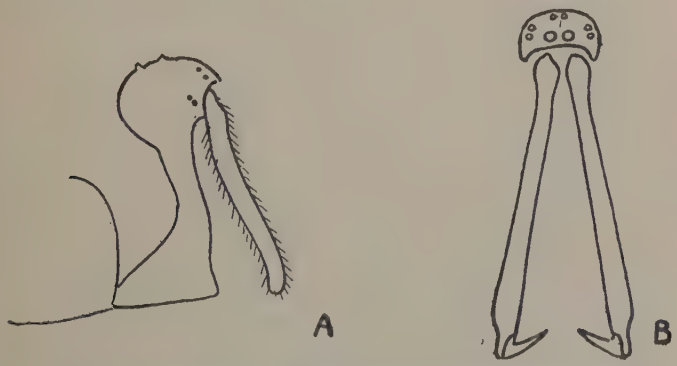


FIG. 14.—Chelicerae of Archaeidae (A) and Landana (B).

The Palpi

The second pair of appendages, the palpi, perform diverse functions. They are six-jointed limbs, the joints being coxa, trochanter, femur, patella, tibia, tarsus. In the *Spiders of Dorset*, Pickard-Cambridge does not separately name the coxa, regarding it as a part of the maxilla and names the remaining five axillary, humeral, cubital, radial and digital. The distal joints are used by young and by female spiders as sensory organs, while in the mature male the femur

Fig. 15.—A Spider's Mouth-parts. L, Lip; M, maxillary lobe; C, coxa; F, femur; P, patella; Ti, tibia; Ta, tarsus.

may be used in stridulation and the tarsus is an accessory to the reproductive system. In addition there is, except in the Mygalomorphae, an endite or inside lobe of the coxa which acts as one of the mouth-parts.

This endite, the maxilla or maxillary lobe, is separated by membrane from the coxa of the limb. Its function is to compress the food particles and squeeze out their liquid contents into the pharynx. Its innermost margin is generally provided with hairs which may be sufficiently dense to form a scopula (Fig. 15) and the fore-edge often bears a serrula

or row of teeth which, doubtless, help in cutting the food. In *Ammoxenus* these teeth are particularly conspicuous.

The main interest of the palpi of spiders lies, however, in the modification presented by the tarsal joint of the male, converting it into the sexual intromittent organ. So remote a separation of this organ from the testes, which lie in the abdomen, is indeed remarkable enough in itself, but in addition the elaborations of these parts are so varied that in no two species are they exactly alike. They provide, therefore, the most trustworthy way of identifying and characterising the males of all spiders.

The study of these organs, and especially of the more complex forms, is by no means easy. Different names have been given by different writers to the same part and many descriptions have been written which do not in fact describe. The palpal organ cannot be analytically studied at all in its normal resting position, it must be expanded and this is achieved by a few minutes' boiling in aqueous caustic potash. The temptation is then to make a microscope slide of the product, and this is fatal, for as soon as the organ is fixed and flattened out, any chance of determining the relations of the parts is considerably lessened. It should be preserved free, in glycerine, where it is always available for manipulation and examination from every angle. Studied by these methods, the forms of the palpi of male spiders open up an interesting inquiry in evolutionary biology.

There are two ways in which the male palp differs from that of the female, apart from the modification of the tarsus, and these are both concerned with the preceding joint, the tibia. The male palpal tibia is relatively shorter than that of the female, at any rate at maturity, and it frequently carries on its outer side, a short process, the "radial apophysis" of Pickard-Cambridge, whose shape is characteristic in each separate species. This makes it a valuable feature in identification. In mating this spur is fitted into a groove in the female epigynum (Fig. 84).

The simplest form of palpal organ is situated near the tip of the tarsus, in a cavity, the alveolus. It consists of a

coiled tube or receptaculum seminis (Fig. 16) in which three parts are recognisable. These are a basal or proximal swollen bulb, the fundus, an intermediate reservoir, and, distally, a dark elongated duct, the ejaculatory duct. This type of palpus gives a clue to the probable course of evolution of the organ. The bulb is evidently a modification of the

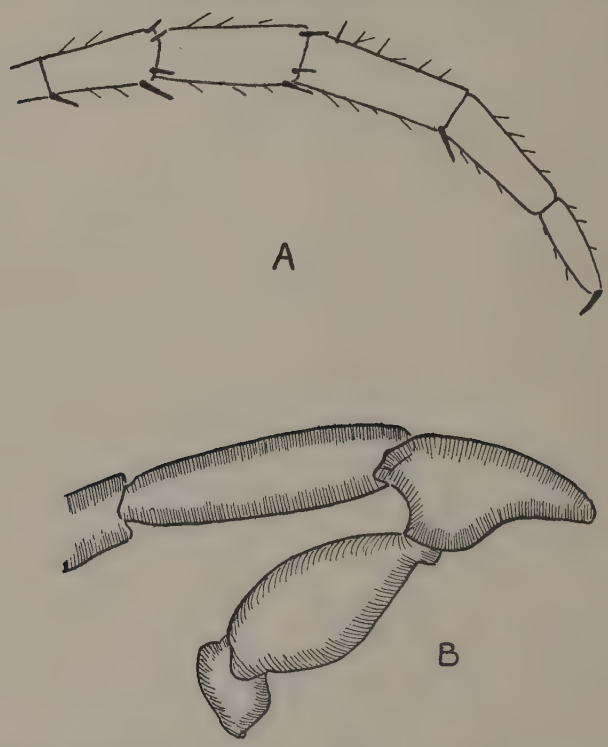


FIG. 16.—A Spider's Palp. A, Female. B, Male—with simplest type of organ.

extreme tip of the tarsus, an invagination of which forms the reservoir, a part which is marked with transverse striations like a respiratory trachea. This interpretation is consistent with the invariable absence of a terminal claw from the male palpus, whereas many females possess a claw in this position.

The first advance from this simple condition is the migra-

tion of the entire genital bulb to the lower side of the tarsus and an increase in the size of the alveolus. The tarsus thus becomes more or less cup-like and is usually renamed the cymbium. At the same time the palpal organ becomes divisible externally in three regions, which may be described as the basal, middle and apical divisions. The apical division is usually called the embolus. The three regions contain respectively the fundus, the reservoir and the duct of the receptaculum seminis. The basal division is united to the alveolus by a membrane which bears a small chitinous sclerite, the petiole. This type of palpus is seen in the Mygalomorphae and is shown in Fig. 17. It is characteristic of this type that the passage from the middle division to the embolus is gradual rather than abrupt.

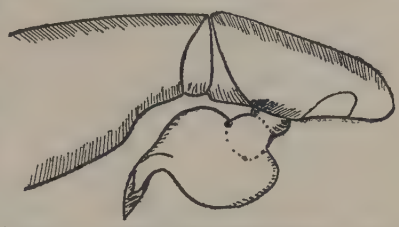


FIG. 17. — Palp of Sipalolasma ophiriensis. A trap-door spider. After H. C. Abraham.

Two changes may be taken as roughly representing the next stage and producing an intermediate type of palpus,

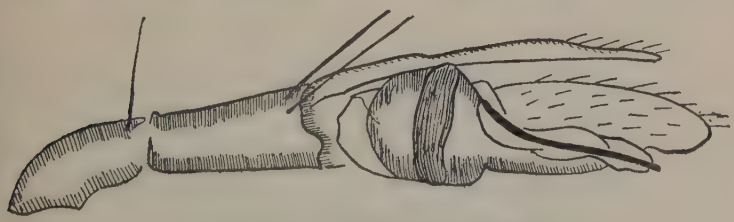


FIG. 18.—Palp of Pachygnatha degeerii.

possessed by many genera of spiders otherwise somewhat widely separated and agreeing only in being the less specialised members of their families. The apical division of the genital bulb becomes divided into two. One of these only is a duct for ejaculation of sperm, and is consequently the embolus proper. The other is called the conductor: its function is protection of the embolus when the organ is

at rest in the alveolus. In the figure (Fig. 18) the darker embolus can be seen passing round and into the coils of the conductor, which is a fairly thick twisted plate, nearly always to be recognised by its membranous nature. The tarsus, too, is sometimes divided into two parts, of which the smaller is called the paracymbium. It is easy to see in Fig. 18, but in many more complicated organs it is much less conspicuous.

In the most conspicuous types of palpi there are elaborations of the appendages of the parts already described, rather

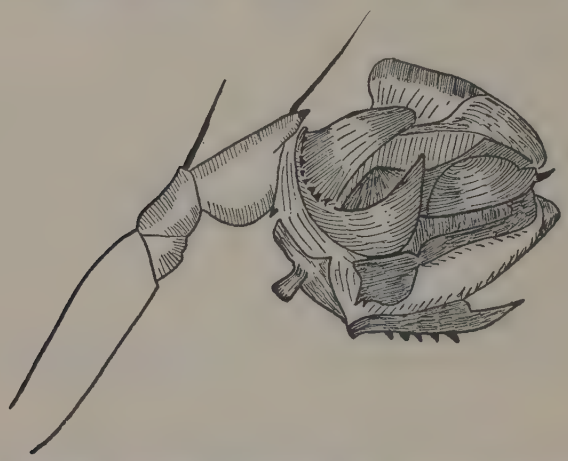


FIG. 19.—Palp of Centromerus sylvaticus. An example showing extreme elaboration.

than a very great development in the parts themselves. As shown in Fig. 19, the three divisions of the bulb are separated by more or less distinct membranous necks. The basal division is attached to the alveolus by a membranous sac, called the basal haematodocha from the fact that at the time of pairing it is distended with blood. It contains, however, no sign of muscular tissue and when the organ is at rest it is invisible, being covered by a ring-like piece of chitin, the sub-tegulum. A similar ring of chitin protects the wall of the middle division and is called the tegulum. From the distal border of this tegulum there arises a chitinous tooth

or appendage, which in some spiders is large and very conspicuous. It has been named the median apophysis, the lamella characteristica, and the scopus. The apical division is subject to the greatest changes. The embolus is composed of two distinct parts, a proximal radix and a distal stipes, and it ends in a strong plate or spike of chitin called the terminal apophysis. But, in addition, secondary haematodochas and extra apophyses may be present, to complete the tale of an extraordinarily complex and remarkable organ.

The Legs

The legs, always eight in number, are seven-jointed and the joints are coxa, trochanter, femur, patella, tibia, meta-

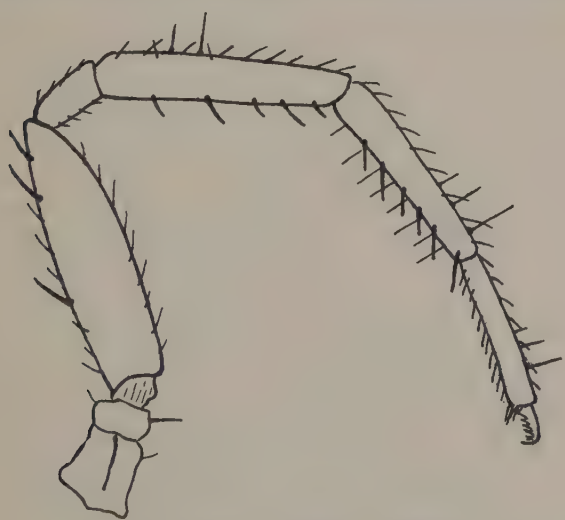


Fig. 20.—Leg of Xysticus cristatus.

tarsus and tarsus (Fig. 20). It is interesting to notice that while these are the old names borrowed from vertebrate morphology, the tarsus has been placed beyond the metatarsus. Pickard-Cambridge calls the joints exinguinal, coxal, femoral, genual, tibial, metatarsal and tarsal, and so produces a confusion when writing of the coxal joint. In a

few spiders false articulations, or rings of softer membrane between the chitinous parts, produce an apparent increase in the number of joints.

Normally each joint is a chitinous cylinder, united by membrane to its neighbours, and each is as a rule straight, save the femur, which is noticeably curved in some species. The ends of each joint are not cut off square, but are so shaped as to allow different degrees of relative mobility between the parts.

The trochanter scarcely moves at all; when it does so it follows the femur, the first long joint, which can move freely upwards and sideways, but not very far downwards. Downward bending is the only degree of freedom of the patella, and the tibia follows the patella, but is capable of a little sideways movement in addition. Like the patella, the metatarsus is confined to downward bending, but the tarsus is able to move freely in all directions. This means that while the leg may be lowered at any joint, it can only be raised by the femur and moved forwards or backwards by the femur, tibia (slightly) and tarsus.

When spiders walk the longest legs, generally the first and fourth pairs, move along the lines of their own directions by vertical movements of the femora. The other two pairs of shorter legs move at right angles to their own directions by longitudinal movement or rotation of the femora. The first and third legs of the near side move together, simultaneously with the second and fourth legs of the off side, the step being completed by a simultaneous complementary movement of the other legs. Such a movement may be presented by four men in Indian file, the first and third marching in step with one another and out of step with the second and fourth. The sideways movement of crab-spiders differs from this since the longest legs are those of the first and second pairs and the rotating motion of the third legs is slight.

The coxa is marked on its pre-axial face with a furrow running along almost its whole length and terminating at a small projection where it touches the trochanter. This

joint has similarly a slight continuation of this groove, and its lower surface is divided by a semicircular furrow into two regions.

The femora of some male trap-door spiders carry small hooks on their inner surfaces. These are a protective device used in mating, when the male spider thrusts them against the chelicerae of the female, gagging her for the time being and so considerably reducing the risks to himself.

It is worth noticing that the legs of spiders take no part in mastication, as do the legs of the Opiliones, for example, and that the palpi alone possess the characteristic Arthropodan "gnathobase."

It has long been customary among araneologists to use the relative lengths of the legs in characterising the various genera, and to express this in a "leg formula," *e.g.* 1.4.2.3. This means that the first pair of legs is the longest, then the fourth, and the third pair is the shortest. A good deal is to be learnt from a careful comparative study of these ratios, as well as of the relative lengths of the separate joints. This work is, however, at present in the course of completion, and its results will be stated elsewhere. A long-familiar fact is, however, the frequent elaboration of the first leg. Owing to its position, this is the limb which must first convey tactile impressions of the surroundings as the spider walks. It is therefore usually the longest and two extreme

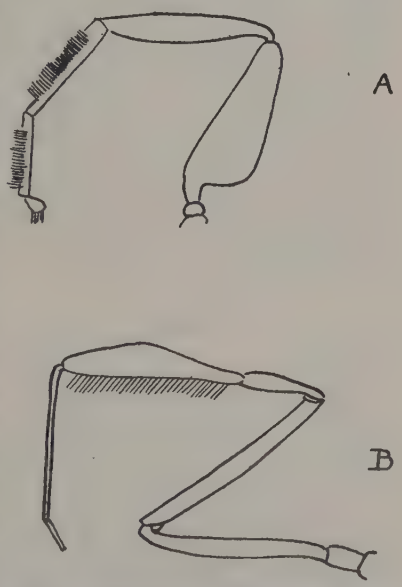


FIG. 21.—Examples of Elaborated Forelegs. A, 1st leg of Palpimanus gibbulus. B, 1st leg of Diolenius phrynoides. After Simon.

instances of its development are shown in Fig. 21. Another feature of the first leg, which will be more fully described in a later chapter, is its decoration in certain male spiders, so that it may be displayed before the female in courtship.

The use which a spider makes of its legs is, therefore, by no means limited to mere walking. Not only are they very efficient assistants to the chelicerae in dealing with captured insects, but, provided as they are with claws, with hairs, with tactile and auditory setae and with the mysterious lyriform organs, they are to be reckoned as the most active organs of the spider's body. A common error describes them as the most useful organs, a statement which overlooks the fact that in so complex a system as an animal's body all parts become useless if only one fails in its function. For instance, a leg must be nourished, supplied with blood, and controlled by nerves. It may, indeed, be said that the spider is sufficiently true to the traditions of the animal kingdom to see with its eyes and to taste, if it taste at all, which is doubtful, with some part of its mouth, but it feels and it hears and it smells with its legs. These last activities are considered with the senses in Chapter IV, the setae and claws are dealt with here.

The Setae

Much of the spider's body as well as its legs, is covered with what would ordinarily be called hairs. Hair in the true zoological sense of a living outgrowth from the skin is, however, peculiar to mammals, and the similar possessions of the spider are better termed setae. Probably all the setae on a spider are more or less developed as sense organs, but some of those on the legs are useful accessories to the spinning organs. On examining a spider it is easy to distinguish hairs of at least three different kinds. The most conspicuous are the stout sharp spines on the legs and palpi, generally described as tactile. The most difficult to distinguish, even under the microscope, are the long delicate acoustic setae,

believed to be receptors of sound waves. These two types are more fully described in Chapter IV.

Intermediate between the extremes of the obviously stout and the very fine, there are many other kinds, often vaguely termed protective, on both legs and abdomen. Several different forms of these hairs are to be found, some are club-shaped, some spatulate, some with branches, some like small spines. In many instances one particular type is limited to a single family. Their exact functions are by no means easy to determine and more attention might well be devoted to them.

It is probable that in some spiders, the body-hairs may exercise a protective function by piercing the skin of any unwary handler and setting up irritation. The occurrence is familiar enough to those who have to do with hairy caterpillars, and it has certainly been shown by some of the large spiders at the Zoological Gardens. It suggests, of course, a cutaneous or subcutaneous gland, the secretion from which flows either through the hollow within the hair or over its surface.

That such glandular hairs may be possessed by some spiders is rendered the more probable by the existence on the tarsi of many hunting and jumping spiders of groups of hairs known as scopulae. These hairs are of the peculiar form shown in Fig. 22, and are often spoken of as tenent hairs. They seem to enable the spider to adhere to horizontal and vertical surfaces, as any one who has tried to shake an *Anyphœna accentuata* out of a test-tube knows full well! Some spiders have a similar tuft or scopula on the metatarsi (Fig. 27).

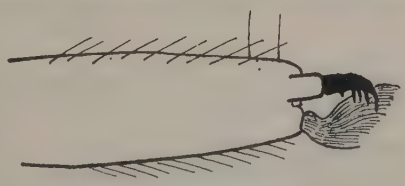


FIG. 22.—A Spider's Tarsus, showing claw and scopula.

Another way of regarding these hairs and spines is to consider not the individual structure, but their arrangement on the spider's body. Leg spines, for instance, are generally

definitely located in superior, inferior, preaxial or postaxial rows, and the number constituting such a row may be constant within the limits of a genus. Illustrations of two such arrangements, possessed by the genera *Zora* and *Ero*, are shown in Fig. 23, where the plan is sufficiently obvious

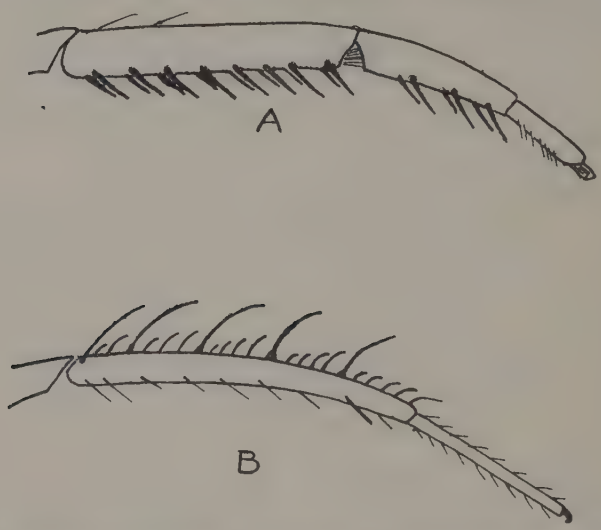


FIG. 23.—Arrangement of Leg-spines. A, Zora spinimana. B, Ero furcata.

to take the eye at once, but the same principle may be extended to all spiders. The most obviously useful of all such groupings is the comb or calamistrum borne by the metatarsi of all cribellate spiders (except the mature males). This is used in combing out the fine strands of silk from the cribellum, the combed threads giving the webs made by these spiders their familiar bluish tinge.

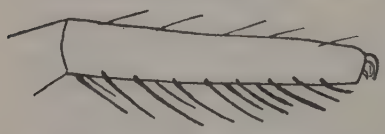


FIG. 24.—Tarsal Comb of Theridiidae.

A tarsal comb is seen in all spiders belonging to the family Theridiidae and these small spiders use it for flinging ribbons or sheets of silk upon a struggling capture, before feeding upon it (Fig. 24).

The Claws

The extreme tip of the tarsus is sometimes called the praetarsus, although as a rule it is not a separate part. From it arise the paired claws which terminate the legs of all spiders (Fig. 25). When the praetarsus extends between the claws, the extension is known as the empodium, and is a valuable part. Sometimes it is unmodified, sometimes it is pad-like, sometimes it carries adhesive hairs, and sometimes it is modified into a third median claw.

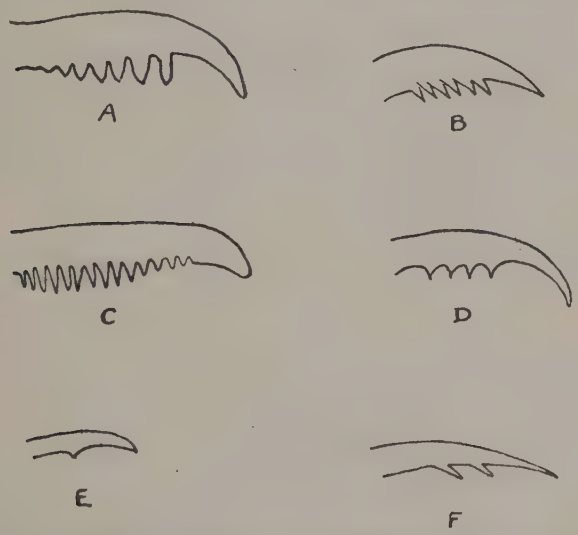


Fig. 25.—Spiders' Claws, showing differences in the number of teeth. A, Sparassus. B, Amaurobius. C, Tegenaria. D, Zora. E, Ero. F, Gongylidium.

This third claw is of importance in classification. It is present in the wolf-spiders or Lycosidae and some other hunting spiders and in certain families of web-spiders.

The paired claws are very hard and sharply pointed, generally curved and provided with a row of teeth on the inside of the curve. The number of teeth varies in different genera and species of spiders, and even, apparently, in the same individual spider with increasing age. In this respect

sex seems to exert an influence, the number of teeth increasing in male spiders and decreasing in females.

Finally, there is a type of structure known as accessory claws present on the tarsi and also on the spinnerets of orb-weaving or Epeirid spiders. These are straight and spine-like, but their lower edge is notched with a few small teeth.

The Spinnerets

The only abdominal appendages persistent in the adult spider are those of the fourth and fifth segments, where they function as the spinning organs—namely, the cribellum, where this organ is present, and the six spinnerets. The cribellum represents the endopodites of the fourth segment, whose exopodites are the anterior or superior spinnerets. The small middle spinnerets are the endopodites of the fifth, and the exopodites of this segment are the posterior or

Fig. 26.—Spinnerets of Hahnia.

inferior spinnerets. The number of spinnerets differs, however, from type to type. In the Liphistiomorphae, the primitive number, eight, is found, occupying the middle of the lower surface, but only the four exopodites are said to be active. In most Mygalomorphae there are four spinnerets, the anterior and median pairs, and in exceptional instances the spinnerets number only two—sometimes the two anterior and sometimes the two posterior.

In most spiders, the spinnerets when at rest form an inconspicuous group at the end of the abdomen and the

smaller median pair are hidden by the larger ones. The relative lengths of the spinnerets in different families are, however, very variable, a difference which seems to be due not so much to the amount of use made of these organs as to the method by which they distribute silk. For instance, in the highest families of spiders, which spin orb-webs, the spinnerets are short and almost unnoticeable. In the house-spiders, which make a flat sheet-web, swaying the abdomen from side to side, the anterior spinnerets are much the longest and can be seen from above like two little tails. In a closely related family, the Hahniidae, the spinnerets form a row and not a group at the end of the abdomen, a unique arrangement. In Mygalomorphae, too, the anterior spinnerets are long; and in a curious family, the Hersiliidae, their length is extreme. Lyonnet has suggested that these tail-like spinnerets may, by virtue of the hairs which clothe them, act as tactile as well as spinning organs—a sort of posterior pair of palpi. The most curious arrangement of all is that of *Cryptothele*, an Asiatic genus, whose spinnerets lie in a mamillary hollow, from which they can be extruded and into which they can be withdrawn.

The individual spinneret is a finger-like organ, jointed in the same way as are the false joints of the tarsi, by rings of softer membrane. The anterior spinneret usually consists of two such joints, but occasionally of three or even four, the median spinneret is unjointed and the posterior spinneret is always of two joints.

It is an important feature of the spinnerets that they themselves are not the actual tubes through which the silk is secreted. The sides of the spinneret are slightly harder than the rest of the abdomen, but the tip is either squarely or obliquely coated with softer membrane, forming a small area described as the spinning field. This field is covered with the battery of minute tubes through which the fluid silk passes, and these tubes are of two main sorts. The smaller ones, called spools or fusulae, consist either of a cylindrical basal portion traversed by a long thin tube or of a slightly conical base with a curved thin tube (Fig. 27).

These are scattered in large though variable numbers over the fields of all spinnerets. They have two uses. Those on the anterior spinnerets produce the little band or transverse sweep of many tiny threads which anchor a spider's lines to the ground, and are known as attachment discs ; while those on the other spinnerets provide the much broader ribbon which the spider wraps round its resisting victim.

The larger tubes, or spigots, are conical in shape and more constant in number and position Their complete

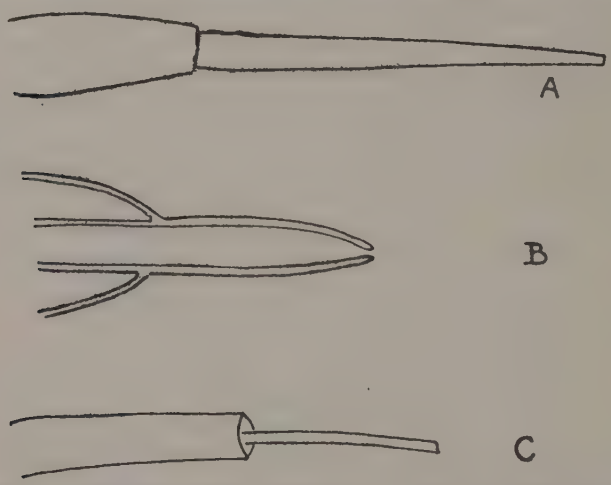


FIG. 27.—Spinning-tubes or Spigots. A, Of cylindrica gland of Tegenaria. B, Of ampullaceal gland of Epeira. C, Of aciniform gland of Epeira. (B, after Apstein.)

distribution among all or even most of the families does not seem to have been worked out, but Warburton (1895) has made a careful study of them in the case of the highest type of spinners, the orb-weavers, Epeiridae, and his results are summarised below.

The inferior, median and posterior spinnerets of Epeira carry respectively one, three and five spigots each. Those on the anterior spinnerets and one of those on each median spinneret provide the foundation lines of the web and the drag-line which many spiders lay down behind them

wherever they go. Four spigots, the two remaining on the median spinneret and two of the five on the posterior spinneret, are used only in the making of the cocoon. The coloured wadding often found protecting the eggs is taken from them. The three other spigots on each posterior spinneret produce not silk, but the glutinous fluid which makes the spiral thread of the web adhesive. Although deposited round the thread at the moment of formation it breaks up from the cylindrical to the more stable spherical form, and beads the line with a regular arrangement of minute globules. These differently functioning spigots are connected with different glands in the abdomen, which will be described in the next chapter.

The Cribellum

The cribellum (Fig. 28) is an oval plate found just in front of the anterior spinnerets in certain families of spiders, but not in all. It is perforated with a large number of minute pores, each of which is the orifice of the duct from a gland. These glands are found only in association with the cribellum itself, and are not represented by any analogue

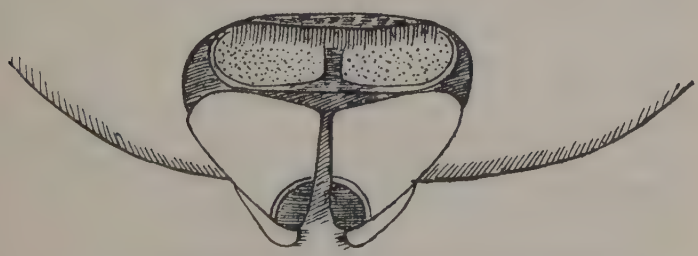


Fig. 28.—The Cribellum and Spinnerets of Amaurobius.

in ecribellate families. The function of the organ is quite clear and may readily be witnessed in many common spiders. The activity of the glands secreting silk through numerous pores, produces a broad ribbon of silk composed of some hundreds of threads. This ribbon is combed out of the cribellum by the calamistrum on the fourth metatarsus

(Fig. 29) and is by that limb laid upon the plain silk strand which the spinnerets are simultaneously producing. The effect is to render the threads of the web more adhesive to struggling insects, to encumber their legs and wings and further delay their escape. It produces also a bluish appearance in the threads of the web as a whole, not by any pigment in the silk, but by interference of the light, the process which gives to soap bubbles and oil-films their evanescent colour. These bluish webs, looking rather

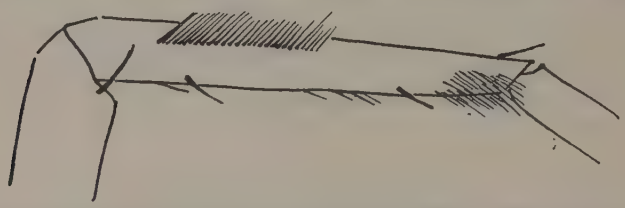


FIG. 29.—The Calamistrum of Amaurobius, showing also a metatarsal scopula.

untidy, like tangled masses of silk, are frequent enough in cellars, on wood palings and gate-posts, where they are spun by spiders of the genus *Amaurobius*, the commonest of the British cribellate species.

A good deal of controversy has been held as to the exact significance of the presence or absence of this organ, a subject which will be discussed in its proper place in Chapter XV. Widely divergent views have been held and cribellate spiders separated from the rest by making them, on the one hand, a separate genus in the same family, and on the other, an entirely distinct sub-order.

CHAPTER III

THE INTERNAL STRUCTURE OF SPIDERS

THE consideration of the internal structure of spiders or of any other animal emphasises, more clearly than does the external appearance, the dual aspect of these anatomical studies. For with each part and organ we are concerned in two ways—its shape and its function ; in other words, with the How-it-is-made and the How-it-works of the animal body, the twin sciences of Morphology and Physiology.

The general plan of the Arthropod may be likened to a hard external tube, from which depend other hard but jointed tubes, the limbs. Through the middle runs another tube, a soft one, the alimentary canal, and the ring-like space between the two tubes is almost wholly filled with blood. This blood-containing cavity is called the haemocoel. In it and freely bathed by the blood lie the various systems of organs—nervous, reproductive, glandular, and excretory. This all-pervading enlargement of the blood vessels, forming a haemocoelic body-cavity, is one of the main Arthropodan characters, distinguishing them very clearly from the Annelida and from all the vertebrates. In these types the perivisceral space is called the coelom, and has a very different embryological origin from the haemocoel. The blood is confined to definite vessels—arteries, veins, and capillaries—and the coelom communicates with the outside world by vessels of two sorts, nephridia or excretory tubes, and coelomoducts, whose original function was to serve for the liberation of the reproductive cells or gametes. But in Arachnida, as in

several other groups, true nephridia are not found, and in such instances the work of excretion is taken over by coelomoducts. The true coelom in spiders is thus found only in inconspicuous hollows in the gonads and in the excretory glands.

With this introduction to the general plan of the Arachnid we may proceed to the different systems in turn.

The Body-Wall

The body wall is characterised by its assumption of both protecting and supporting functions—it is in fact an exo-skeleton. A section (Fig. 30) shows it to be made up of three layers, of which the outermost, or cuticle, is not composed of cells, while the other two are cellular. The pigmentary matter, to which the colour and most of the pattern of the spider is due, is contained in the extreme superficial layer. Below this the cuticle has a stratified appearance, where it may be comparatively soft, as on the abdomen, or may be hardened, as on the legs and cephalothorax, by impregnation with chitin.

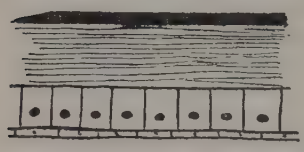


Fig. 30.—Section of Body-wall. A, External cuticle, with pigment. B, Internal cuticle, with chitin. C, Hypodermis. D, Basement membrane. Partly after Comstock.

Chitin, an invaluable material, found in many invertebrates and a few vertebrates, is a nitrogenous organic compound. More precisely, it belongs to the scleroprotein group of the polypeptides. Its chief characteristic is its resistance to ordinary reagents, and thus it is well suited to form a protective covering to the living animal.

If the body of a spider be boiled in dilute caustic potash for about a quarter of an hour, the whole of the internal tissues are dissolved and the chitinous exo-skeleton is left as a hollow case. The colour can be bleached from it by hydrogen peroxide or any other weak oxidising agent, when the residue can be dissolved in pure hydrochloric

acid. On dilution with a considerable proportion of water the chitin is reprecipitated. It is a colourless amorphous powder, unaffected by alkalis or by any of the ordinary organic solvents, and soluble only in concentrated mineral acids. When boiled with strong acids, it is hydrolysed to acetic acid and glycosamine. The formula $C_{15}H_{26}N_2O_{10}$ has been suggested for it, when this action would be :

$$2C_{15}H_{26}N_2O_{10}+2H_2O \rightarrow 3CH_3COOH+4CH_2OH(CH.OH.)_3CH.NH_2CHO$$

Below the cuticle is a layer of cubical epithelium known as the hypodermis. This is interrupted only where one of its cells has become modified into a hair-producing cell or trichogen. The body of the trichogen sinks below the hypodermal level, through which the shaft of the hair or spine rises, piercing the cuticle which surrounds it by a diminutive embankment and forming a trichopore (Fig. 31).

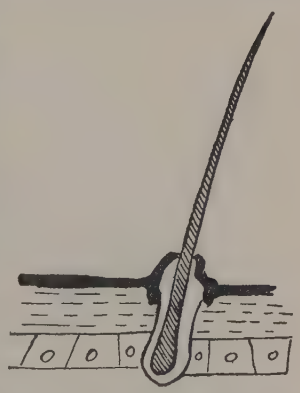


Fig. 31.—Section of Seta-producing Cell of Epeira diademata.

On the inner side the hypodermis is lined with pavement epithelium known as basement membrane. Thus cuticle, hypodermis, and basement membrane compose together the body-wall.

The Endoskeleton

But there is also need for internal skeletal structures, chiefly for the attachment of muscles. The most important of these is the endosternite in the cephalothorax, a plate of chitin which it is not very difficult to dissect out, clean, and examine. Its shape is shown in Fig. 32. When in position, the endosternite lies below the stomach and above the ventral nerve ganglia. Many muscles are attached to

it, some of which are connected to the stomach, some to the body-wall, and some to the limbs.

It was mentioned in the last chapter that small depressed points due to muscle attachments are usually found on the abdomen. When these are produced internally into solid prominences, the latter are known as apodemes. The endosternite has originated from the development and fusion of four pairs of such apodemes from situations opposite the legs, so that morphologically speaking it is a part of the body-wall.

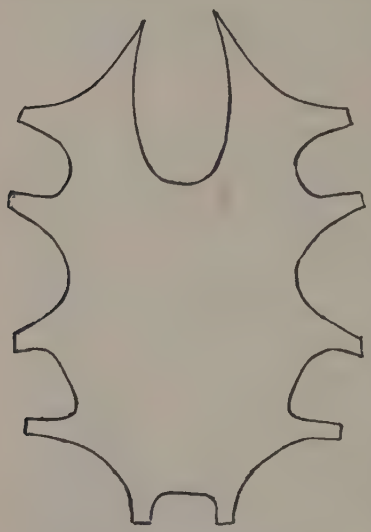


FIG. 32.—The Endosternite.

Three small separate apodemes are found in the abdomen. Since the appendages of the abdomen are so reduced, the internal skeletal structures and internal muscles are reduced too.

Muscular tissue is characterised by the elongated thread-like shape of its cells, which possess the power of contraction in a high degree. The cells are separated by the minimum of matrix and in certain instances (voluntary muscles) are recognised by their transverse stripes.

Students of elementary biology have long been accustomed to make their preparations of striated muscle from the crayfish, the typical transverse marking being more easily seen in arthropod muscle than in amphibian or mammalian. The muscles of the spider are similar in this respect. When fresh they are very soft and almost colourless; on fixing and staining with suitable histological reagents the fibres and striations are quite easily made out.

This muscle tissue fills up much of the cephalothorax,

where it has chiefly to do with the alimentary canal and the movements of the limbs (Fig. 33). The pharynx is fixed to the sides of the body by several pairs of muscles, and one median muscle, the retractor of the pharynx, is attached to its upper end. The sucking stomach, which depends for its action on alteration of its size, is well furnished with muscles. Several vertical muscles connect its upper surface with the under side of the groove of the cephalothorax, and others are joined to the endosternite. The limbs are necessarily composed largely of muscle within,

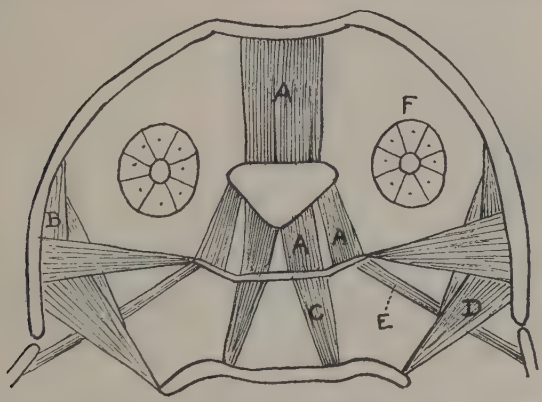


FIG. 33.—Vertical Section through Cephalothorax. A, Dilators of stomach; B, muscle which retracts leg; C, muscle which lowers leg; D, muscle which advances leg; E, muscle which raises leg; F, caecum of gut. After various authors.

while at the coxal end several muscles join the limb both to the body wall and to the endosternite. The arrangement of the leg muscles is shown in Fig. 34, which was drawn from the fourth leg of an *Amaurobius*, dissected by G. T. Pitts and M. L. Meade-King, two of my pupils at Malvern.

In the abdomen the circular and longitudinal layers of muscle in contact with the hypodermis, which form so conspicuous a feature in types like the earthworm, are reduced to mere vestiges. The chief mass of abdominal muscle lies close behind the pedicle, connected to it and

to the anterior of the three abdominal apodemes. Muscles from the lung-books and reproductive orifices are also

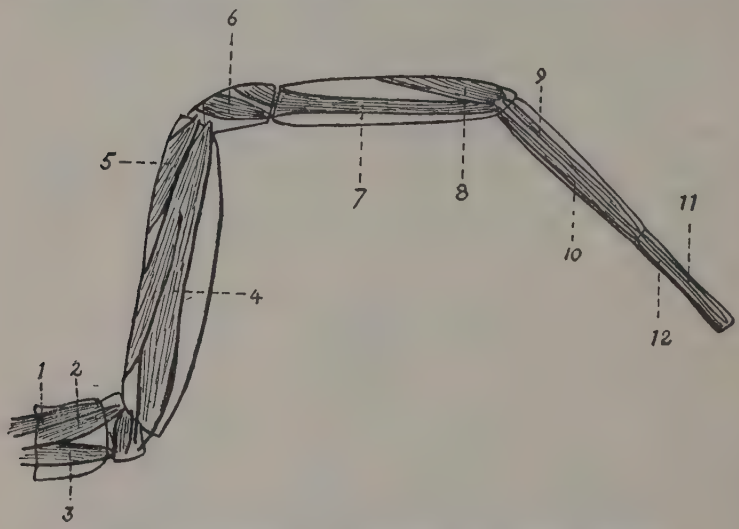


FIG. 34.—Leg-muscles. 1, Extensor; 2, moves trochanter; 3, flexor; 4, flexor of femur, and extensor of patella; 5, flexor of patella; 6, lateral movement of tibia; 7, flexor of metatarsus; 8, extensor of metatarsus; 9, extensor of tarsus; 10, flexor of tarsus; 11, 12, claw-muscles.

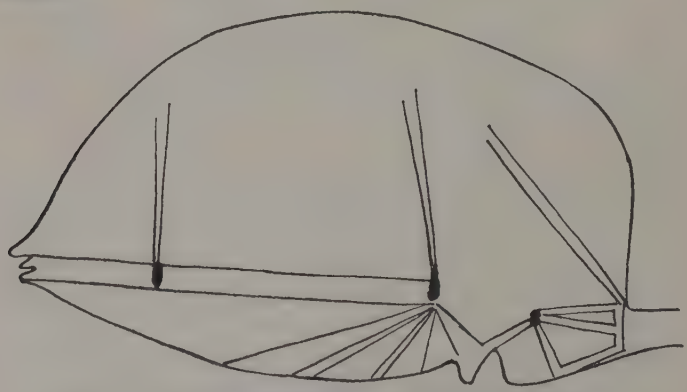


FIG. 35.—Abdominal Apodemes. After Schimkewitsch.

attached to this apodeme. Another series of longitudinal muscles run to the spinnerets from the posterior apodeme.

Lastly, the depressed points on the upper surface of the abdomen are connected to the middle and posterior apodemes by vertical muscle strands (Fig. 35).

The Alimentary Canal

The alimentary canal, to which reference has been made, is in spiders a complicated system charged with imbibing, storing, and digesting the food. It is of a type peculiar to Arachnida, and does not closely resemble that of any other class of invertebrates.

The mouth is an extremely small aperture, difficult to discern clearly. Lying directly above the labium, and in close contact with it, is a flattened cone of tissue called the rostrum. If the rostrum and labium are separated the lower surface of the former is seen to be covered with a chitinous plate, the epipharynx. Opposed to it, on the upper surface of the labium is a corresponding plate, the hypopharynx. The epipharynx and, in Mygalomorphae, the hypopharynx, are marked with fine grooves forming, when placed against one another, the stomodaeum up which the food rises into the oesophagus, partly by surface tension, partly by the sucking action of the stomach within. The epipharynx is also marked with fine transverse striations and edged with minute teeth.

The alimentary canal of spiders agrees, however, with that of most other Arthropoda in being divisible into three regions, of which only the intermediate part is lined with epithelium and is absorptive in action. The fore and hind portions are derived from the invaginations of the exoskeleton at the anterior and posterior ends of the embryo, forming the stomodaeum and proctodaeum respectively.

The fore-gut, or stomodaeum (Fig. 36), consists of pharynx, oesophagus, and sucking stomach. All these parts are lined with chitin and the structure of their sides is the same as that of the body-wall, with which they are in continuity.

The pharynx rises almost vertically between the

epipharynx and the hypopharynx. The curvature of the epipharynx produces a space which is occupied by a median gland, the pharyngeal gland. This is a minute oval mass of secretory cells with a duct leading to the end of the pharynx, near its junction with the oesophagus.

The oesophagus is a much easier part of the canal to obtain in a dissection and it has long been well known. It is a slightly curved tube, whose internal chitin is thickened

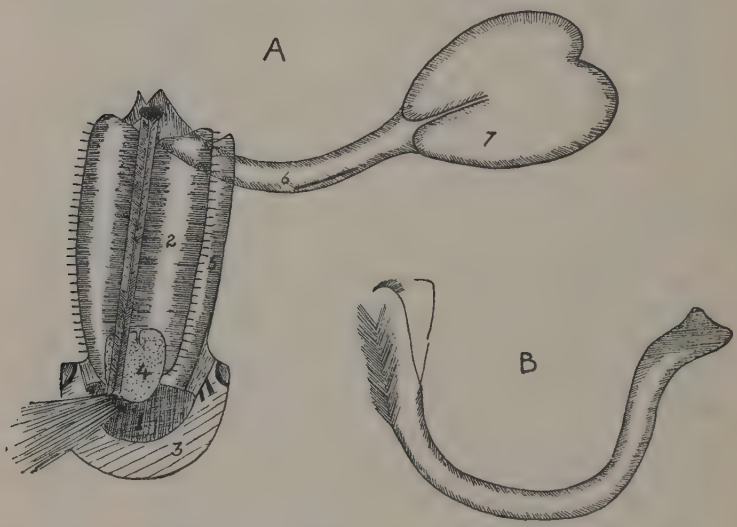


FIG. 36.—Fore-gut of Spider. A, Epeira diademata. 1, Rostrum; 2, epipharynx; 3, labium; 4, pharyngeal gland; 5, hypopharynx; 6, oesophagus; 7, sucking stomach. B, Oesophagus of Tegenaria atrica, showing difference in curvature.

above and striated on the sides in a characteristic way. Its lower surface is thinner and less conspicuous so that the part is often compared to an inverted gutter.

The sucking stomach is misnamed since it has none of the functions of a stomach, but is rather to be compared to a pump drawing in the food from outside. For this reason it is often referred to as the "so-called stomach," but this seems a meticulous usage and has not been followed here. It is formed by a widening of the oesophagus, and lies on

the endosternite. Nearly the whole of its upper surface is hardened, forming a leaf-shaped shield with its point forwards and with a median ridge below, so that its cross-section is T-shaped. This ridge is a continuation of the dorsal thickening of the oesophagus.

The sucking organ is enlarged by the perpendicular muscles attached to its shield and to the median groove of the carapace. It is closed by a series of semicircular compressor muscles attached to the edges of the shield and to the endosternite. There is no muscle in its own composition.

The mid-gut, or mesenteron, is the true absorptive region, and it is in this part that spiders show their most striking departures from the more general Arthropodan type of an unbranched tubular canal.

To make food valuable to the spider, the process of digestion must involve such chemical changes as will make the food soluble, and so able to pass in solution through the intestinal walls into the blood which will distribute it to the tissues. In different animals there are different devices by which the absorption of the food-products is rendered as complete as possible, either by increasing the time spent in the absorbing region or by increasing the absorbing surface area in contact with the food. The former type is illustrated by the dogfish, whose comparatively short intestine encloses a spiral valve. In travelling down the turns of this spiral the food takes a very much longer time than it would in passing directly from end to end. The second method is illustrated by the earthworm, whose intestine possesses a dorsal infolding or typhlosole. This largely increases the absorptive area in contact with the finely divided soil which is passing down it. The two methods are combined in mammals and many others, whose small intestine or ileum is greatly elongated, until its total length becomes many times greater than that of the animal itself. The spider possesses two such devices for securing an increased efficiency, which are unlike those of any other type of animal.

The alimentary canal leaves the sucking stomach as a narrow tube directed towards the pedicle. Before reaching the pedicle there arise from its sides two diverticula or blindly-ending tubes which run forwards above the endosternite as far as the poison glands. In some spiders these diverticula meet in front forming a complete circle, but as a rule their ends, though lying close together, are separate. In addition to this, four short lateral caeca arise from the

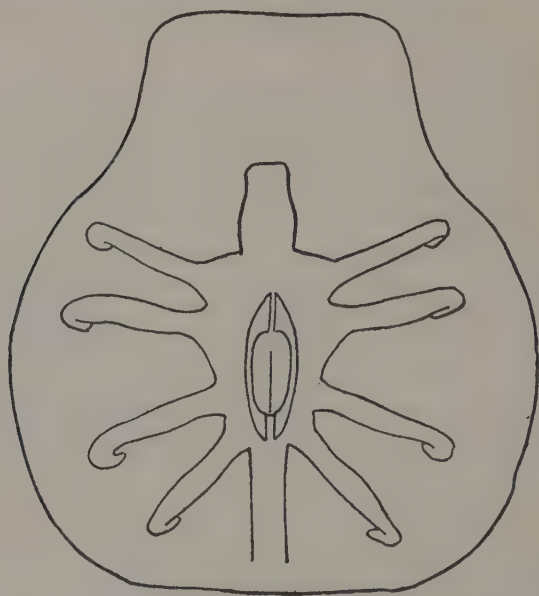


FIG. 37.—Fore-gut from above, showing caeca directed towards legs. Partly after Leuckart.

outer side of each diverticulum in the directions of the legs. They may be prolonged some little way into the coxae, or they may be bent downwards and inwards under the ventral nerve mass which lies beneath the oesophagus (Fig. 37). The liquid contents of these caeca has a digestive action on meat. They therefore probably act as a reservoir for this fluid.

The mesenteron then passes back through the pedicle

and shortly after entering the abdomen curves upwards and widens. In the upper surface of this wider portion there are usually four orifices leading into the complex system of branched tubules which form the abdominal gland. This gland occupies the greater part of the inside of the spider's abdomen, nearly the whole of the upper and lateral portions. It is penetrated in all directions by the Malpighian tubes, and its branches ramify round the heart and intestine in a bewildering confusion. It has long attracted the attentions and speculations of anatomists and has been successively described as a stomach, a fat-body, a liver, and a pancreas. The truth would seem to be that it functions in two distinct ways. It acts as a digestive gland, secreting a ferment upon the food, but also as a reservoir, for the food-products pass into the tubes themselves. Thus they swell out, and a spider after a large meal becomes bloated to an extent which would be quite impossible if it were due only to the expansion of the mid-gut itself. It is, of course, not very usual to find the food entering the digestive glands instead of merely receiving their secretions through a duct, and the result is that it grants the spider power to receive relatively enormous quantities of food at a time. This is stored and gradually absorbed by the abdominal gland, so that long periods of fasting can be survived.

The mesenteron passes into the proctodaeum without any great change in size, but the latter, in addition to its chitinous lining, is surrounded as well by a layer of muscle cells. It bears on its dorsal surface an enlargement or hollow, the stercoral pocket, where faecal matter accumulates in the form of a milky fluid in which float small black particles. The rectum is a straight tube opening at the anus, which lies at the end of a small tubercle, behind the posterior pair of spinnerets.

The digestion of the food is of necessity followed by three consequences. A small proportion of the nutriment gained is stored as fat, the rest must be conveyed to all the tissues by the blood, and the waste matter must be eliminated.

The adipose tissue of spiders consists of cells containing droplets of fat. These are found in three situations. A layer of fat-cells lines the interior of the cephalothoracic caeca, and the space in the abdomen between the branchings of the abdominal gland is filled with fatty material. Lastly, a layer of fat-cells lies in the cephalothorax between the nerve ganglia and the sternum.

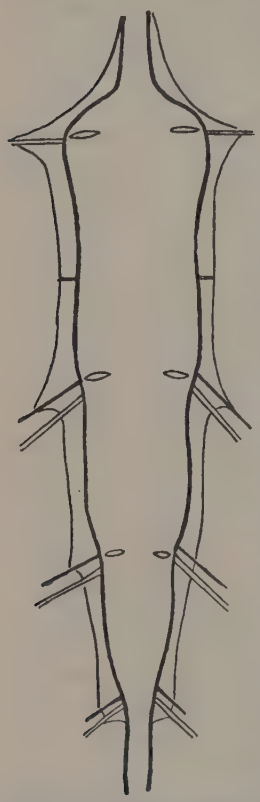


Fig. 38. — A Spider's Heart. Partly after Causard.

The Vascular System

In mammals such as ourselves, the characteristic of the circulatory system is that there are two independent blood streams through the heart, one of purified blood going to the tissues of the body, and one of blood which, after its return from the circuit of the body, is going to the lungs to be oxygenated. In spiders, as in other Arthropoda, there is but one course of blood through the heart, and one circuit of the body. This circuit, too, is incomplete. The blood is not at all points confined to vessels: there are no capillaries and the internal organs lie bathed in blood.

The heart (Fig. 38) is a straight tube, conical in shape, lying in the dorsal part of the abdomen, sometimes quite close to the skin and sometimes embedded in the alimentary caeca. It is chiefly composed of muscle cells, the majority of which are transversely arranged, but a few are longitudinal. Outside the muscle is a coat of connective tissue fibres. The heart is simple within, not divided by valves into chambers. It lies in a thin-walled sac, the pericardium,

which surrounds it at some little distance so as to leave a pericardial space between the two. Both heart and pericardium are held in position by a complex system of numerous ligaments, above, below, and at the sides.

The pericardial space is filled with blood which enters the heart through three pairs of apertures or ostia—four pairs in Mygalomorphae. These ostia are provided with valves which prevent the blood from re-entering the pericardium from the heart, so that it is forced to pass out of the heart by the arteries which lead from it.

The aorta, or forward prolongation of the heart, dips down and passes through the pedicle into the cephalothorax. Here the posterior dorsal arteries arise from it, to

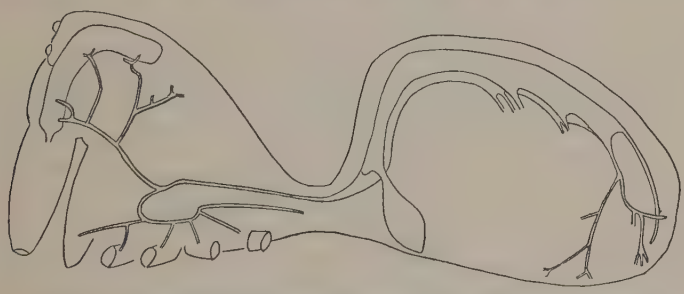


FIG. 39.—Side View of Blood-System. After Petrunkevitch.

supply the muscles of that region. Behind the stomach it divides into two branches which lie between the sides of the stomach and the cephalothoracic caeca. Near the front end of the endosternite there arise two forwardly directed cephalic arteries, which supply blood to the eyes and poison-glands, while the Aortic vessels dip suddenly downwards and form a centre from which blood vessels run to the palpi and legs (Fig. 39).

The lateral arteries arising from the heart are eight in number in Mygalomorphae and six in most other spiders. They distribute blood among the majority of the organs contained in the abdomen (Fig. 40).

Posteriorly the heart is continued into the caudal artery. This branches among the spinnerets and silk glands.

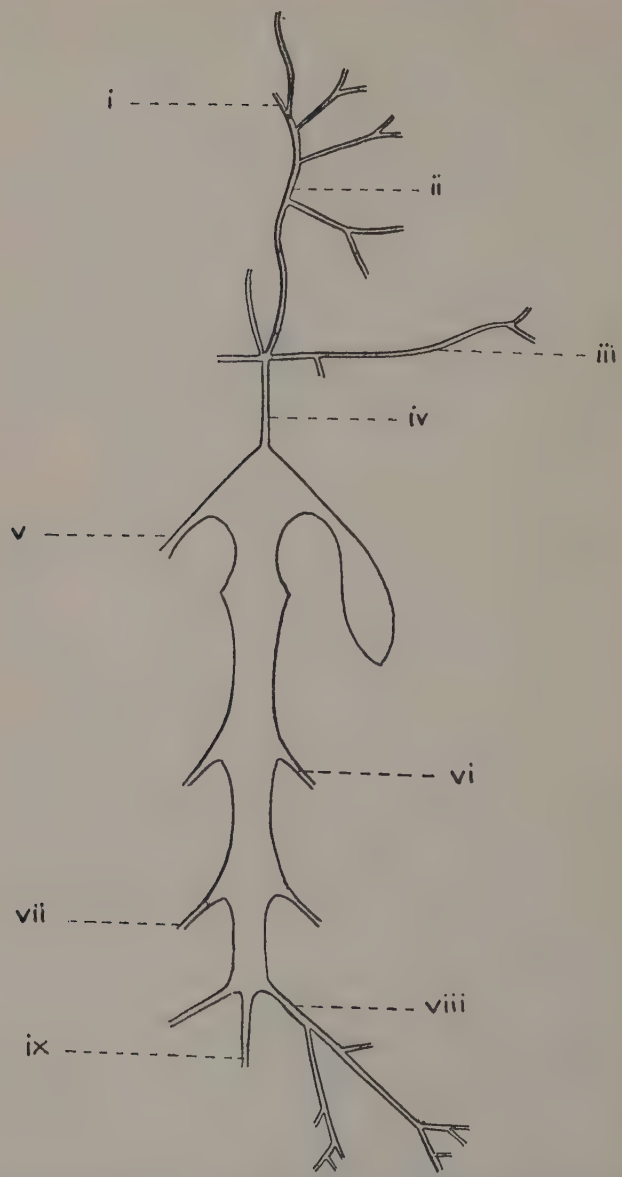


FIG. 40.—Dorsal View of Blood System. After Petrunkevitch. i, Mandibular artery; ii, cephalic artery; iii, dorsal artery; iv, aorta; v, pulmonary vein; vi, diverticular vein; vii, ventral abdominal artery; viii, posterior artery; ix, recurrent artery.

The blood does not return by veins. It is collected in rather vague channels called lacunae, which deliver it to spaces called sinuses. There are six of these sinuses, three in each division of the body. The three in the cephalothorax are longitudinal spaces lying parallel to one another, close to the sternum. Two of the abdominal sinuses are also near the ventral surface, the third is below the pericardium. All these sinuses conduct the blood to the lung-books, where it is re-oxygenated by the air entering through the leaves. By two pulmonary veins, or, in Mygalomorphae, by four pulmonary veins, the blood now flows back to the pericardium, whence it re-enters the heart by the ostia. These pulmonary veins are the only vessels in the spider to be called veins. They are similar in constitution to the cardiac ligaments which hold the heart in place. Causard has indeed suggested that the other lateral ligaments are reduced veins, which have lost their original function of conveying blood and become mere ligaments.

The Blood

The blood which courses in the system is a very pale blue opalescent fluid, which may be obtained in sufficient quantity for examination by cutting through the middle of a joint of a spider's leg. If smeared on a microscope slide, fixed and stained, it may be seen to contain a number of clear rounded corpuscles, in which a nucleus is not easily visible. These doubtless have the same function as the colourless corpuscles or leucocytes of vertebrates' blood. That is to say, they attack and ingest invading bacteria, thus checking their multiplication in what would otherwise be a very favourable medium. There is nothing corresponding to the red corpuscles of man. The plasma in which the leucocytes float contains in solution a pigment known as haemocyanin.

Haemocyanin is of similar constitution to haemoglobin; the formula $C_{867}H_{1363}N_{223}CuS_4O_{258}$ has been suggested for it, and it will be noticed that it contains copper instead

of iron. It is a pigment widely distributed among invertebrates, being present in the blood of most Crustacea and Mollusca, as well as Arachnida. When reduced or deprived of oxygen it is almost colourless, but oxy-haemocyanin has a more or less pronounced blue tinge.

The Respiratory System

We have more than once had occasion to point out that the Arachnida stand in many respects intermediate between Crustacea and Insects, and in the respiratory system this is again noticeable. Most Crustacea breathe by gills and most Insects by tracheal tubes. Among Arachnida gills, lungs, and tracheal tubes are found.

Spiders, being land-living creatures, have no gills. Their lungs are of a peculiar type, known both as lung-books and book-lungs, to be presently described. Lung-books and tracheae usually exist together in the same spider, but there are exceptions to this. In the more primitive suborders of spiders, the Liphistiomorphae and Mygalomorphae, and in one family, the Hypochilidae, of the Arachnomorphae there are two pairs of lung-books and no tracheae. The majority of spiders possess a pair of lung-books, and either a single or a paired tracheal opening, while in an exceptional family, the Caponiidae, there are two pairs of tracheal openings and no lungs.

The lung-books were mentioned in the last chapter as conspicuous pale patches in the epigastric region. Each is a large hollow space, communicating with the external air by a small pore. The space contains from fifteen to twenty of the " leaves " which give it its name. Each leaf is attached to the side of the space in front and at the sides, being free posteriorly (Fig. 41). It is a fold of the body-wall and is therefore double, the two halves being kept apart by numerous vertical supports. The top surface of the upper lamella of each fold is provided with vertical knobbed spikes, which serve to keep the leaves apart and to allow the air to circulate freely between them. The

hollows within the leaves are in direct communication with the blood sinuses of the abdomen. The blood thus enters the leaves, oxygen is taken in and carbon dioxide is passed out by direct diffusion through the thin surfaces. The two lung-books always communicate with one another by a transverse spiracle.

The tracheae are always paired structures, even when they open at a single median spiracle. Among Insects the tracheae form an elaborate system of branching tubes, conveying air to the tissues, and even, so fine are their ultimate branches, to the individual cells of the body. The blood of these creatures has therefore lost its respiratory

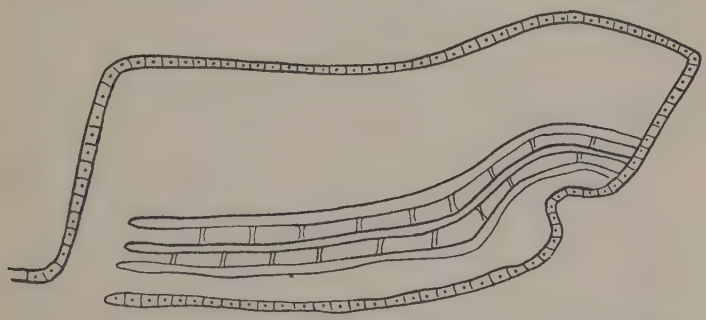


FIG. 41.—Transverse Section through a Lung-book. (Only three leaves are shown.)

function and possesses no oxygen-carrying pigment. As has been seen, this is not so with Arachnida. Their tracheae, like those of Peripatus, diverge in bunches at intervals from the main tube, but do not branch, save in exceptional instances. This very interesting method of oxygenating the tissues—by direct supply of air from without—seems to have been evolved independently by several classes of Arthropoda, as a result of their leaving the water and coming to live on land. Sir Ray Lankester has pointed out that tracheae are most numerous where blood vessels are fewest. They may be two modifications of the same tissue-elements, the tracheae containing air instead of blood.

The Excretory System

Excretion of nitrogenous waste-products is performed in spiders by Malpighian tubules and coxal glands.

A pair of fine branching tubes opens into the intestine near the stercoral pocket and are known by the name of their discoverer, the Italian zoologist Malpighi, as Malpighian tubules. Similar vessels to these are found in most of the Arthropoda, but seem to be not all homologous, or identical in origin. Those of insects originate in the ectoderm and arise from the proctodaeum, those of scorpions, of some crustaceans (Amphipoda), and probably those of spiders are of endodermal origin and join the mesenteron. It would seem that the possession of these tubes does not necessarily imply a phylogenetic relationship, but rather that they represent a method of excretion readily and variously evolved on passing from an aquatic to a terrestrial or aerial life. They are absent from *Limulus*.

There is, however, no doubt of their function. An extract in water of a sufficient number of Malpighian tubes can be shown to contain uric acid—a characteristic nitrogenous waste-product in animals. Moreover, since their secretion is neutral and sodium can readily be detected in it, it is probable that the uric acid is present as sodium urate. Urea seems to be absent from spiders, but there is ample evidence of the renal functions of the Malpighian vessels.

The coxal glands have been mentioned above in connection with the vanishing coelom as a type of excretory organ. Our knowledge of these rather remarkable organs is due to the admirable work of Buxton, who has studied their varying forms in many of the orders of Arachnida.

Coxal glands are found most fully developed in the more primitive spiders of the sub-orders Liphistiomorphae and Mygalomorphae, and in gradually simplifying conditions in the higher families of the sub-order Arachnomorphae. In the highest families of all they exist in an extremely reduced state.

In their typical form, the glands, as seen in the Mygalomorphae or trap-door spiders, consist of two large excretory sacs, lined with cubical or flattened epithelial cells. These cells have the power of excreting solid particles, such as those of carmine, if this be injected under the animal's skin. They are normally found to contain solid particles, which are probably crystals of urates in the process of excretion.

The sacs lie outside the endosternite opposite the coxae of the first and third legs. They both discharge their products into a convoluted tube, the labyrinth, whose many coils occupy the space from the first to the fourth coxa. The labyrinth is lined with excretory epithelium, but apparently does not excrete solid matter. From its posterior end there runs forwards a straight tube, the internal limb of the labyrinth, lying inside the convoluted portion. From the internal limb short exit-tubes open to the exterior in the body-wall behind the first and third coxae, where the orifice can be opened and closed at will. These parts are shown diagramatically in Fig. 42.

The two sacs are probably homologous with the large nephridia in segments 6 and 7 of *Peripatus*. In the highest sub-order of spiders, the Arachnomorphae, three different types of coxal glands are found, all of which agree in having lost the sac and outlet of the third leg, retaining only that of the first.

The first stage is seen in the families Dysderidae, Oonopidae, and Sicariidae, which for various reasons may be taken as representatives of the most primitive living Arachnomorphae, as will be shown in Chapter XV. In spiders of these families the sac retains its previous character, but the labyrinth does not. It runs posteriorly from the sac as a straight tube as far as the fourth leg, where it turns inwards, widens and runs forwards along the endosternite to its outlet. Only in exceptional genera are there any loops in the labyrinth at its posterior end.

The second stage includes the majority of the sub-order. The capacity of the internal limb is increased by extensions above and below between the second and third

and between the third and fourth coxae, and by a dorsal one opposite the orifice. Its function is probably to be

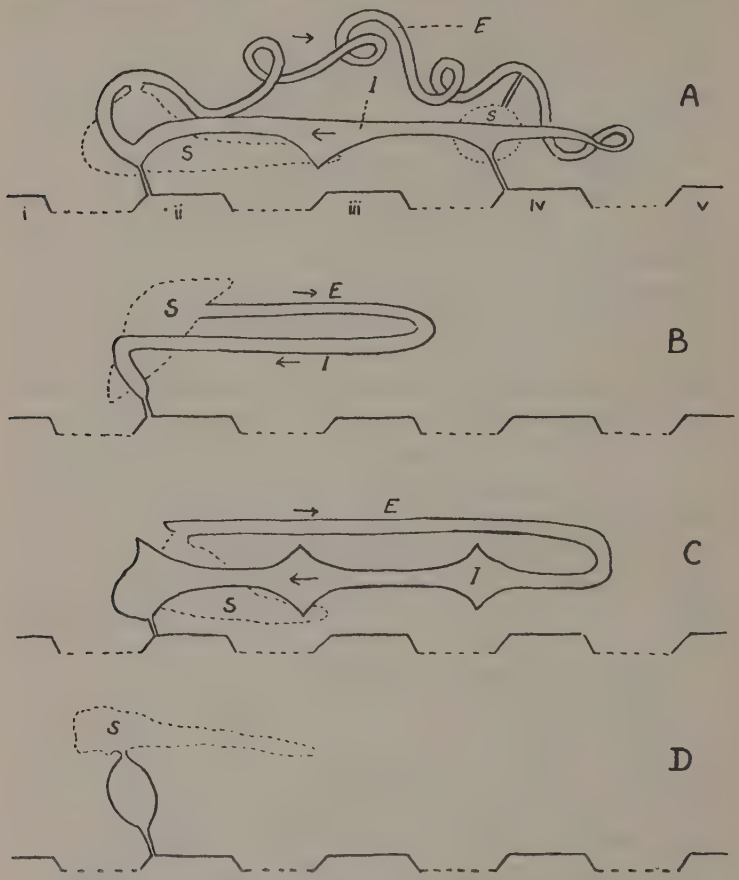


FIG. 42.—Diagram of Coxal Glands. A, Arrangement in Mygalomorphae and Liphistiomorphae. B, Arrangement in Dysderidae, Oonopidae, etc. C, Arrangement in Lycosidae, Thomisidae, Drassidae, Salticidae, Agelenidae, etc. D, Arrangement in Epeiridae, Theridiidae, Pholcidae, and Filistatidae. S, Saccule ; E, external tube of labyrinth ; I, internal tube of labyrinth ; i, coxa of palp ; ii–v, coxae of legs i–iv.

compared to that of a bladder, for it has no excretory powers.

In the third and highest stage there is very little of the

labyrinth left and the saccule opens almost directly to the exterior.

It is at first sight remarkable that the evolution of the families of spiders should be thus accompanied by an apparent degeneration of an important system. But degeneration is not the correct term for these changes. In the third stage noted above the sac and orifice are actively functional and show no signs of resigning their duties. The changes in form seem to be rather in the nature of a simplification following greater efficiency of the parts retained. The very interesting suggestion was made by Bernard in 1897 that the excretory products of the labyrinth have become utilised by the silk glands. That an excreted substance, originally waste matter on its way from the body, should be utilised for some purpose is not without parallel in other creatures. Chitin, mentioned at the beginning of this chapter, is possibly of such a nature ; so, too, is the bile of the vertebrate liver. It should obviously be possible to test this suggestion by experiment, for if it be true, a coloured substance injected under the skin of a living spider should make itself manifest in the threads of coloured silk which that spider ought to produce. The practical difficulty in such an experiment is the extreme dilution which the pigment would suffer, and which would make its subsequent visibility in the silk extremely small.

The Reproductive System

The internal reproductive organs of spiders are not very complex. The testes of the male lie parallel to one another in the abdomen below the alimentary canal. They are tubular in form, closed behind, and continued in front into a pair of much coiled tubes, the vasa deferentia. These unite at their extremities to form a very short vesicula seminalis, leading directly to the single median orifice in the epigastric furrow.

The ovaries occupy a corresponding position, but they are much larger, especially when the eggs are nearly mature,

and thus they are much easier to find. Because of the ovarian follicles, which project from their surfaces, they are always compared to bunches of grapes. The eggs pass through the narrow neck of the follicle into the hollow within the ovary, whence they travel forwards to the oviducts. The oviducts are straight wide tubes, which unite to form a so-called uterus above the vagina. The vagina is lined with the chitin of the body-wall, and leads directly to the epigyne above described. Opening laterally out of the vagina are two narrow ducts leading to the spermathecae in which the spermatozoa received from the male spider are stored until the eggs are laid. In some spiders this is the only entrance to the spermathecae, in others there are independent openings to the exterior constituting part of the epigynum. Spermathecal glands may also be present.

The Nervous System

The spider's nervous system presents a simple external form—remarkably simple when we consider its great responsibilities.

When a sense-organ—an eye, a hair, or a spine—is stimulated by the reception of some impulse from without, it transmits to the central nervous system the fact of its stimulation. The central nervous system must appreciate the import of the impulse received, determine the appropriate action and initiate the response. The nervous system must also discharge the important function of correlating the activities of every organ of the body so that all may work as a harmonious whole and respond to changes in the environment in a way which will secure safety for the individual and continuance for its race.

In the phylum of segmented worms from which the phylum of the Arthropoda is derived, the central nervous system consists of an unbranched double nerve-cord running from end to end of the body below the alimentary canal. In each segment the cord swells to form a nerve-

knot or ganglion from which paired nerves arise. The "brain" is represented by two supra-pharyngeal ganglia above the pharynx, joined by nerves to two sub-pharyngeal ganglia below. These connecting nerves are called circumpharyngeal commissures and form a "nerve-collar" through which the pharynx passes.

The form of the nervous system found in the adult spider (Fig. 43) has been considerably modified from this primitive arrangement, and, as in other examples of the same process, the modification consists in an apparent reduction in the number of ganglia, owing to their fusion with one another. Thus the "brain" of the spider is a composite syncerebrum, composed of three lobes. One of these is the so-called prostomial ganglion and two were the ganglia of the prosthomeres, or segments which in development have passed in front of the mouth. In the same way the ganglia of the other segments of the cephalothorax have fused instead of remaining separate, and the nerve-collar through which the fore-gut passes is thick and conspicuous.

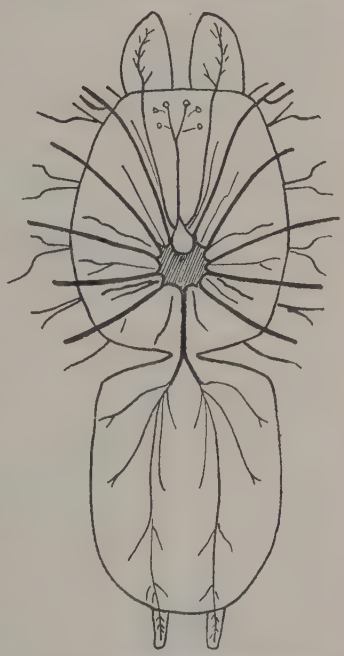


Fig. 43.—The Nervous System. From Dahl after Blanchard.

The ganglia of the abdomen are evanescent, like the segments themselves. In very young spiders there is a stage in which as many as six ganglia are present along the floor of the abdomen, but these disappear in the course of development, and in the adult there is no trace of a ventral nerve-cord in the abdomen.

Glands of the Cephalothorax

The secretory glands of the spider's body are the poison-glands, the mysterious maxillary glands, and the silk-producing glands.

The poison or venom with which spiders numb their prey is secreted by a pair of large sac-like glands, situated in the first joint of the chelicerae of Mygalomorph spiders and in the fore part of the cephalothorax of the true or Arachnomorph spiders. It is possible that these glands are modified salivary glands, which, since the spider's food

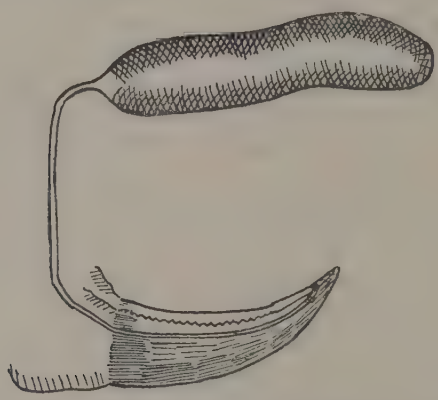


Fig. 44.—Poison gland and Duct, opening at end of fang.

is easy of digestion, have taken on a more sinister function instead of degenerating. The reservoir of the gland is quite easy to dissect out in any large English spider, but what taxes the skill of the dissector to the utmost is the extraction of both gland and duct unbroken. The latter, which is very fine, passes down the two joints of the chelicera, and opens, as already described, just within the point (Fig. 44).

The secretion is of an acid character. It is rapidly fatal to the small insects which form the spider's usual catch; its effects on larger animals are varied, while its effect on man has given rise to many years of controversy

which has only lately begun to give place to confidence and certainty. The poisoning powers of spiders are more fully discussed in Chapter VI. As will there be seen, many experiments on the virulence of the poison have given conflicting results, and this is probably due, not to imperfect experiment, but to the fact that in some instances the bite was indeed innocuous. The act of biting does not automatically expel the poison from the gland. Fig. 44 was drawn from a mounted preparation stained with borax carmine, and it illustrates the fact that the gland is covered with spirally-arranged muscle-cells. It is therefore probable that injection of the poison is under the control of the spider. When it was withheld, the bite was no more serious than a prick with a needle.

The maxillary lobes or endites of the palpi seem to be mainly concerned with acting as auxiliaries to the chelicerae, and the glands they contain are of uncertain function. Within each maxilla is a group of ten or twelve cylindrical glands in communication with a plexus of wide intracellular tubes—that is, tubes running through, not between, cells which have a particularly large nucleus (Fig. 45).

From their position it would seem to be obvious that these glands serve for the predigestion of the prey, or are at any rate concerned in some way with the nutritive functions of the spider. However, they do not react to microscopic stains as do digestive glands, and they do not resemble poison glands. Professor Warren has suggested that they may be preening glands, for when the spider cleans itself, it may be seen to draw its legs and palpi through the maxillae as if transferring fluid from them to its body surface. Of course it is possible that, like the saliva of a cat, the fluid secreted by the maxillary glands may serve both purposes. Another possibility is that the secretion of these glands prevents the spider's legs from sticking to its own web. This would explain the care with which the spider periodically anoints itself, and a recent observation of my own tends rather to confirm this view. A small orb-weaver, belonging to the very common species

Meta segmentata had had a long struggle with a vigorous crane-fly. The insect was at last tied up at the lower edge of the web and much labour was then devoted to hauling it up to the resting place to be eaten. The final raising of the fly was preceded by cutting the viscid lines of the web, to which one or two legs were still adhering, and it was immediately after severing these threads and before proceeding to anything else that I saw the spider

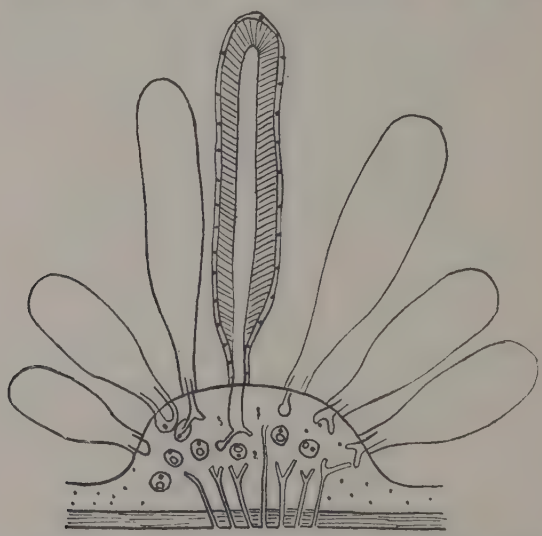


FIG. 45.—Diagramatic Section of Maxillary Glands and Plexus. (After Warren.)

pause and pass the four legs of its first two pairs through its maxillae. It seemed very much as if contact with the viscid lines of the web had made it necessary to re-coat the legs with the maxillary secretion.

On the other hand, the possibility that other virtues may be found in this substance is indicated by the fact that spiders which spin no webs, and those whose webs contain no viscid threads, have also the habit of pulling the legs through the maxillae.

The Silk Glands

We may fitly conclude this chapter with an account of the silk glands. Silk is used for several different purposes by different animals, and it is produced from different parts of their bodies. Caterpillars, for example, spin silk from a modified salivary gland near the mouth, and ant-lions from a modified Malpighian tube near the anus, while the silk glands of spiders are, as already suggested, probably modified coxal glands of abdominal limbs. Clearly, therefore, silk glands in the different orders of Arthropoda are not related to each other; the silk-producing habit has arisen independently in the several groups.

The silk glands of spiders are, as may easily be imagined, of considerable complexity in creatures whose lives depend on their functions. Seven different kinds of glands are to be found possessing orifices on the spinning organs. These are:

1. The Aciniform glands.
2. The Pyriform glands.
3. The Ampullaceal glands.
4. The Cylindrical or Tubuliform glands.
5. The Aggregate glands.
6. The Lobed glands.
7. The glands of the cribellum.

No spider possesses all seven kinds of glands, but all possess the first three. The cylindrical glands are possessed by all female spiders except those of the families Dysderidae and Salticidae. The aggregate glands are found only in the three most highly specialised families, the Theridiidae, the Linyphiidae, and the Epeiridae; and the Theridiidae alone possess lobed glands. Lastly, the cribellum glands are, of course, found only in association with that organ.

The aciniform glands are, as their name implies, berry-like in appearance, each "berry" being composed of a cluster of small round sacs opening into a common duct. The number of glands in each group is about a hundred in

the Epeiridae, but often fewer in other families. There are four such clusters, one to each median and each posterior spinneret, the ducts are short, and the glands lie just inside the abdomen above the spinnerets.

Corresponding to these, the superior spinnerets have each a cluster of pear-shaped or pyriform glands, which also number about a hundred in the Epeiridae and fewer in other families. These six short multiple glands are used when a large quantity of silk is required in a short time. This is the case in the making of the swathing bands or ribbons wrapped round the prey and the short transverse band of silk threads called an attachment disc, which anchors a thread of silk to the ground. The former function is the task of the aciniform glands, and the latter of the pyriform glands—facts which may readily be confirmed by observation. Careful watching of a spider performing these actions (preferably in a glass tube) will show from which spinnerets the silk threads are proceeding. The pyriform glands, which are not difficult to dissect out, are readily distinguished from the others because the distal end of the glands, next to the duct, appears darker than the rest after treatment with some stains, but not with all. Fig. 46 shows this.

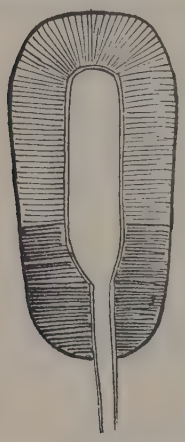


Fig. 46.—A Pyriform Gland.

The ampullaceal glands, which are the remaining type common to all spiders, are generally four in number, although in some spiders there are six, eight, or even twelve. They lie much further forward in the abdomen, nearly in the middle of the lower portion. Their shape (Fig. 47) is that of an ovoid sac drawn out at one end into a long thin coil, and at the other into the long duct. The four ducts open at spigots on the inner side of each of the anterior and median spinnerets. The use of these glands is to supply a continuous thread for a sustained time, in which

activity the sac, or ampulla, to which they owe their name, is probably a help, acting as a kind of reservoir. The framework and radial threads of the orb-web and the drag line, which hunting-spiders leave everywhere behind them, is produced from these glands. It follows that such threads consist of two or four components. Normally these threads are divisible into two halves and two only, since they are spun from the superior spinnerets, but when extra strength is required the thread is quadrupled by reinforcements from the median spinnerets.

The cylindrical or tubuliform glands are of interest because they provide the only instance of a sexual difference in the silk glands. Their number is usually six, but more may be present in some families: in male spiders they are fewer and may be altogether absent. They occupy a position on the base of the abdomen between the ampullaceal and pyriform glands and they open at a spigot on the outside of each median spinneret and at two spigots on the inside of each posterior spinneret. These glands, which are much the easiest to dissect out in any female spider, are tubular in shape as their name implies, and the tube may be more or less convoluted. They produce the silk from which the cocoon is made, including the coloured wadding which is wrapped round the egg-sac—indeed, this coloured material may sometimes be seen stored in the lumen of the gland in a mounted preparation. The Dysderidae and Salticidae, which have no cylindrical glands, do not spin a proper egg cocoon.

FIG. 47.—An Ampullaceal Gland.

The ampullaceal and cylindrical glands are composed of a layer of cellular secretory epithelium inside, covered with peritoneal membrane. The former alone is continued into the duct, a fact which distinguishes these glands from the aciniform and pyriform. This is shown in Fig. 48 which was drawn from a double-stained preparation, made by L. W. Spratt, one of my pupils at Malvern.

The function of the aggregate or tree-shaped glands is problematical. They are found only in the three highest families, the Linyphiidae, the Theridiidae, and the Epeiridae, whose species possess six of these glands, two smaller than the other four. They lie near and usually above the cylindrical glands and are irregularly-shaped branching masses, characterised by projecting caeca on their surfaces. The proximal part of the duct is also similarly studded with knots of cells. The three glands on each side open together on the inner side of each inferior spinneret. While the function of these glands is uncertain, it is generally believed that they supply the very elastic silk of the spiral thread in the orb-web and the viscid drops which coat it. Such threads do occur, though rarely, as components of the webs made by members of the other two families which possess aggregate glands.

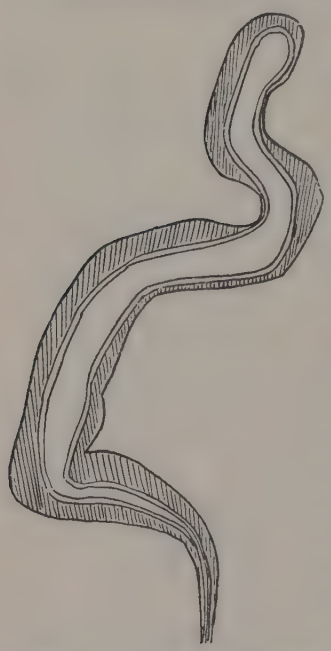


Fig. 48.—A Cylindrical Gland.

The lobed glands are peculiar to one family, the Theridiidae. In the chapter on external structure, this family was mentioned as possessors of a comb of stiff hairs on the tarsal joints of the fourth pair of legs. The combs are used

in a special method of attack and defence which this family alone has adopted, and which consists of combing out ribbons of silk from the spinnerets and throwing them over the insect as it struggles in the web. This band of silk is supplied by the lobed glands. They are two or four in number, and open on the posterior spinnerets by short ducts, so that the glands are only just within the abdomen. They are broad, irregular masses of cells, larger than the aciniform and with a smoother surface. Since they have virtually the same function as the aciniform glands, it is not surprising to find that the number of the latter is much smaller in the Theridiidae.

The cribellum glands are most difficult to dissect, as they are very small and are grouped in large numbers close to the cribellum, through whose pores they open. They supply the additional fine threads which the calamistrum combs out.

Looking back upon our consideration of spider anatomy as a whole, we see that it is a highly organised body showing numerous adaptations to the rather specialised mode of life which the spider leads. The most obvious of these are the extreme development of the sense of touch, the localisation of the senses of smell and hearing on the same active limbs, the increase of storage-room round the alimentary canal, and the elaboration of the silk-producing glands.

Moreover, all these separate systems act in harmony, a fact which we have ascribed above to the governing influence of the nervous system. It should, however, be noticed that in vertebrates some of the harmonising is due to another agent, the so-called " chemical messenger " or hormone. A hormone is a complex compound secreted by an organ or by a special ductless gland directly into the blood stream, which distributes it to all parts of the body. Thus it reaches other organs, where it usually promotes a special activity. The most familiar instance is that of the hormone secretin. When food in the course of digestion passes through the pylorus from stomach to intestine, the lining of the latter

produces secretin. This is conveyed to the rest of the body by the blood stream, and when it reaches the pancreas it stimulates the secretion of the pancreatic juice. Thus the activity of the pancreas is stimulated at the appropriate moment.

Many such hormones are known, but their presence in invertebrates like spiders has not yet been proved. It is, however, possible that they exist, and that they help in harmonising the activity of the various systems and in influencing the behaviour of the individual spider.

CHAPTER IV

THE SENSES AND SENSE ORGANS

In all but the very lowest animals there are some portions of the body specialised for the receipt of information from without. The stimulating external cause is of a physical nature—an ether wave, an air vibration, or a material contact—which excites no activity save in the particular sense organ suited to its reception. The eye-spots of Protista, the cnidocils of *Hydra*, the delicately tactile prostomium of the earthworm are instances of such organs in lowly creatures, which seem not to be endowed with the full complement of sense organs as we know them. However, it is worth while noticing that such definite organs are not always a necessity. The simplest of all Protozoa, *Amoeba*, has none ; but it can appreciate light and warmth and probably the smell of distant food. The possession of sense organs is a consequence of bodily complexity and division of labour resulting therefrom ; it is a measure of the degree of specialisation of the race.

Spiders possess very distinct organs of sight and touch ; they smell by a method of which it is impossible to speak so decidedly ; perhaps they can hear and taste.

The Eyes

The majority of spiders have eight eyes, but a number have six only. The Ceylonese spider, *Tetrablemma*, already mentioned as the possessor of skeletal plates on the abdomen, has four eyes. *Hexablemma*, another spider with the same abnormal characters, discovered in British East Africa

in 1920, possesses six eyes. A South American genus, *Nops*, consists of nine species with only two eyes. The cave-dwelling spiders of the genus *Anthrobia* have no eyes.

John Blackwell, the founder of the study of British spiders, proposed during the last century a division of spiders into tribes based on the number of eyes they possessed. Such a classification, which at the time seemed useful and obvious, was not a natural one and had to be abandoned when systems were based on a more complete knowledge. The six-eyed spiders of Britain do happen to form a more or less natural group, but many foreign species with eight eyes are at least as closely related to them as they are to one another.

Spiders' eyes are situated on the forepart of the cephalothorax, and so distributed over its curved surface that some look vertically upwards, some forwards, and some sideways. In some species they are grouped on a small eminence, and sometimes this eye-bearing projection rises relatively high and gives the spider a very remarkable appearance (Fig. 3).

In the greater number of species the eyes may be considered as comprising two rows of four, but in some instances a first row of four is followed by two rows of two. It is important to notice the eye arrangement, because this feature is frequently used in the classification of the families and genera. The rows of eyes, designated as anterior and posterior, are seldom straight; more often they are either procurved, that is, curved with the convexity backwards, or recurved, with the convexity forwards.

Owing to its convenience, as well as to the weight of years of use, this method of description is not likely to give way readily to the more natural one recently put forward by Professor Petrunkevitch. As he says, "the arrangement of eyes has been studied entirely by systematicians and not by morphologists," and he introduces the distinction between direct eyes and indirect eyes. The middle eyes of the front row, or anterior median eyes, as they are usually called, are the direct eyes. It is seldom

difficult to see that these two eyes are in some way different from the others, a point to which we shall return. We have mentioned already that the part of the spider's head in front of the mouth consists of two fused segments. The direct eyes belong to the first segment and receive their nerves from its ganglion; the indirect eyes all belong to the second segment. The optic lobe of the ganglion of this segment is composed of three parts, one above the other, each part supplying a nerve to an eye. The dorsal nerve supplies the lateral eye of the first row, the middle nerve the median eye of the second row, and the ventral nerve the lateral eye of the second row. Thus there is a pair of direct eyes and a first, second, and third pair of indirect eyes. Two arrangements for the indirect eyes are possible. They may form an incurved row, that is, a curve convex on the outside, in which case the third indirect eyes are the posterior median eyes and the posterior row is procurved; or they may form an excurved row, convex on the inside, when the posterior median eyes are the second indirect eyes and the posterior row is recurved. Fig. 49 illustrates these alternatives. Thus from a scientific point of view it would be more correct to speak of incurved and excurved rows of indirect eyes rather than of procurved and recurved rows.

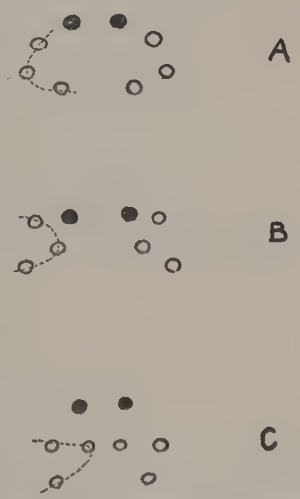


FIG. 49.—Curvature of Indirect Eyes. A, Incurved. B and C, Excurved. In A the posterior median eyes are the third indirect eyes. In B the posterior median eyes are the second indirect eyes. In C the posterior median eyes are the first indirect eyes.

Spiders are sometimes caught in which some of the eyes are much below their usual size, or even altogether missing, so that a normally eight-eyed spider has but seven or six eyes. In his early book, *Researches in Zoology*,

Blackwall records seven such cases, and four more have been mentioned by Falconer more recently. These eleven may be summarised thus :

1. Xysticus cristatus.	July, 1835.	Direct and second indirect eyes absent.
2. Theridion varians.	June, 1852.	Third indirect eyes absent, second very small.
3. Meta segmentata.	August, 1842.	Left second indirect eye absent, right very small.
4. Trochosa leopardus.	?	Right direct eye absent.
5. Amaurobius atrox.	September, 1842.	Left third indirect eye absent.
6. Meta segmentata.	Autumn, 1842.	Right second indirect eye very small.
7. Bathyphantes concolor.	March, 1835.	An extra eye between the direct eyes.
8. Undetermined.	1910.	Totally blind.
9. Walkenaera acuminata.	November, 1908.	Totally blind.
10. Hilaira excisa.	?	First and second indirect eyes missing on one side.
11. Tiso vagans.		"At various times, partially blind specimens."

While there is a sporadic distribution among the different families of spiders, there is apparently a greater tendency for imperfections to manifest themselves in the indirect eyes, and especially the second, than in the direct eyes. The seventh case is of especial interest, as being the only one in which an extra eye is recorded ; moreover, this extra eye was centrally placed, preserving the symmetry of the eye group.

A phenomenon which seems to be somewhat rarer is the apparent possession of sixteen eyes. A *Neriene bituberculata* showing this was found by myself in Malvern on April 27, 1925. The arrangement is shown in Fig. 50. The diagram, showing how the extra eye-pattern is reversed, affords the explanation. The part of the cast caput bearing the eyes must, at the time of the last moult, have turned over and stuck to the new cuticle while the latter was still soft. The only other instance of this of which I have heard was in an American specimen sent to the late Professor

W. Bateson as an example of reduplication of the eyes—which it is not.

In outward appearance the eyes of spiders are simple ocelli, which means that they have a uniformly smooth surface, not broken up into numerous facets, as are the large eyes of insects. In many spiders it is obvious that the eyes are of different types, for some appear black and others pearly-white or pale yellow. The two types of eye are generally described as diurnal and nocturnal respectively, as if some of them were intended for use in the daytime, while the others took over the duty at night. The evidence for this is slight—indeed it is little more than a deduction from internal structure, for there are internal differences in the structure of the eyes.

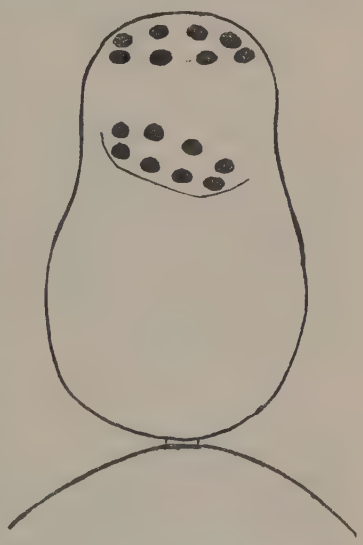


FIG. 50.—A Spider "with Sixteen Eyes."

The cornea of the eye is but a portion of the cuticle, shaped to form a double convex lens, and of course free from hairs and pigment so that it is transparent. As the cuticle is shed when the spider moults, the lenses of the eyes are shed too, and during this process the spider must be temporarily blind. The hypodermis, already described, is continuous beneath the lens, and the retina lies below the hypodermis. The visual cells of which the retina is composed are elongated in form and each has a process running to the optic nerve. But the characteristic of the visual cell is the presence of a pair of hard bodies known as optic rods, which lie adjacent to one another and form a distinct layer in the retina. In the direct eyes this layer is next to the hypodermis and above the nuclei of the visual

cells: hence the dark appearance of the so-called diurnal eyes. In the indirect eyes the optic rods form the base of the eye (Figs. 51 and 52).

One final structure completes the essentials of the indirect eyes, and this is the tapetum. A tapetum is present in the eyes of cats and of many moths, whose eyes are familiarly said to "shine in the dark." It is a reflecting layer whose supposed function is to reflect light after it has entered the eye so that it passes again through the visual cells and so increases the visibility of objects in a dull

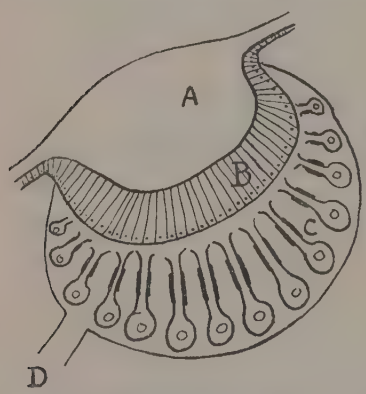


FIG. 51.—A Postbacillar Eye. Simplified diagrammatic section. A, cornea, forming lens; B, hypodermis; C, retina, composed of visual cells; D, optic nerve.

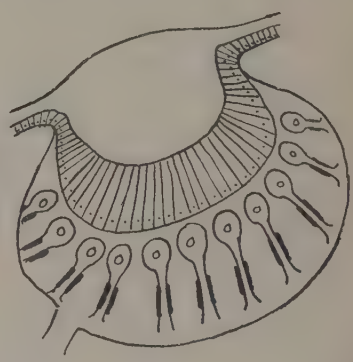


FIG. 52.—A Prebacillar Eye. The optic rods are not next to the hypodermis, but at the base of the eye.

light. The tapetum in spiders is composed of a basal layer of cells containing small crystals, which make the reflecting surface. This is what generally causes the so-called nocturnal eyes to appear paler than the diurnal eyes, but in many eyes in which a tapetum is present, the distribution of pigment within prevents the eye from looking bright. A tapetum is never present in the direct eyes, and these eyes have one other peculiarity—an eye-muscle from the back of the eye to the body-wall.

It is perhaps this muscle which is responsible for a puzzling phenomenon connected with these direct eyes.

Sometimes when looking at a living spider one sees the colour of these eyes change, slightly but unmistakably, from a darker to a lighter shade, or vice versa. When seen in the living but apparently quite motionless spider, it is impossible to avoid the impression that it is due to internal movements under the control of the spider's will, and as such it was first described. It is, of course, possible that this may be so and that the change of colour may be produced by the eye muscles causing some part of the back of the eye to rotate in the optic capsule, and it is also possible that this may enable the spider to look in another direction. It is, in fact, difficult to imagine what other purpose it could fulfil, and it is noteworthy that the action is most readily seen in jumping-spiders, whose direct eyes are very large and certainly keen-sighted. It has also been seen in crab-spiders, and in trap-door spiders, which have not so keen a sight. On the other hand, the same colour change may be seen in the dead spider if the body be tilted very slightly, and this makes it probable that the whole phenomenon is only due to a difference in the angle at which the light falls on the spider's eye and is reflected therefrom. This was the view of the Rev. O. Pickard-Cambridge.

Vision

Keenness of vision differs very considerably in spiders. It is only to be expected that jumping and hunting-spiders should have better sight than those which spend their time waiting for the vibration of their web and which catch their prey largely by the help of the sense of touch. This has led to the widely held but rather unjustified opinion that such spiders have so poor a sense of sight as to be, to all intents and purposes, blind. A secondary deduction, which, however, may have more truth in it, is that one of the chief uses of the spider's eyes is to enable it to distinguish night from day, and so to moult, spin, and lay eggs under cover of darkness.

But as long ago as 1880, Pickard-Cambridge in his

Spiders of Dorset, described how he had several times seen spiders drop on a thread from their usual position in the middle of the web to secure an insect passing underneath. This observation has been more than once confirmed by later workers and shows that even typical web spinners have a certain power of vision.

Rainbow, an Australian araneologist, published in 1898 the results of some experiments which have a direct bearing on the subject of vision in hunting-spiders. He found that crab-spiders, the family Thomisidae, whose habit it is to lurk in hiding-places and to make darts upon passing insects, possessed but poorly-developed power of vision. They could detect their prey at a distance of half an inch only, and not more. When the insect, previously tied to cotton, was jerked out of that range, they seemed to be at a loss and were unable to follow its more distant movements. The behaviour of spiders of this family when mating bears out this conclusion. The male grabs at the female with his chelicerae, thus securing that she does not get out of sight after he has found her.

Wolf-spiders, hunters by nature, showed a much keener power, illustrated in particular by two observations of spiders in natural circumstances. A specimen of *Lycosa godeffroyi* leapt upon and caught a beetle three inches away, although there was a tuft of grass between the spider and its prey; while a *Dolomedes neptunus* caught "at a considerable distance" prey which closely resembled in colour the sea-wrack on which it was hunting. Following up these observations by experiment, Rainbow found that both species could see clearly at five inches and faintly at eight.

A hunting-spider was seen by McCook to leap upon a fly crawling upon the side of its cage and leap back again to the spot to which its drag-line was attached. McCook emphasises this particular instance because it showed that the spider was not only endowed with sight, but also with the ability to estimate speeds and distances with an accuracy sufficient to enable it to land upon moving objects. This

power was also shown by a captive *Pisaura mirabilis* which lived under my own observation. As I described in 1916, a fly flying at some speed along the cage was caught by the spider, which suddenly reached up as the fly passed above it and took it in its jaws as neatly as a cricketer making a catch in the slips.

As has long been known, jumping-spiders have the keenest sight. Dr. and Mrs. Peckham's well-known accounts of the courtship of this family give ample proof of their ability to recognise their mates up to a distance of eight or ten inches. Rainbow showed by experiment that *Attus volans* and *Attus splendidans* could see clearly to seven inches. When we consider the large size of the eyes of these spiders, as well as their mode of life, this is not surprising.

The general conclusion which may be drawn from the recorded experiments and observations is that some spiders can see quite well, but that in others which, because they live in webs, rely more on their sense of touch, the ability is not quite so great.

Colour Vision

Related to this subject is that of the appreciation of colour by spiders. Dr. and Mrs. Peckham were the first to experiment on the sensitiveness of spiders to colour by building a cage of pieces of glass so that the spider within had a choice of freely communicating red, green, blue, and yellow compartments. Various spiders were confined in this cage; whenever they came to rest the colour in which they were found was recorded; the spider was then disturbed and made to choose its resting-place again. From time to time the cage was cleaned of all threads of silk and the order of the colours was changed. The result of all experiments was very conclusive, being,

Red	181
Yellow	32
Green	13
Blue	11

There seems to be no doubt that some spiders at any rate have a very decided preference for red Moreover, it was found that if a spider was blindfolded by coating its eyes with paraffin, it showed no preference for any colour. When placed in the blue quite close to the red, it showed no inclination to move into the colour which had previously proved so attractive. These experiments might well be repeated with a greater variety of species—all the spiders in Dr. Peckham's experiments were wolf-spiders.

The Spines

The existence of setae of various degrees of stoutness, and their arrangement in definite situations on the spider's body, has been described already in Chapter II. Of these setae those which have the best claim to be considered as possible sense organs are the strongest and the most delicate.

The stout and conspicuous spines are probably among the more important organs of touch. They originate, as

Fig. 53.—Palp of Male Leptyphantes minutus.

do all the rest of these setae, from a trichogen or hair-producing cell below the cuticle and are characterised by their strength, by the fact that their bases are often surrounded by a little tubercle of chitin, and by their mobility. The interior of these spines is filled with cytoplasm.

The tubercle from which they sometimes rise is well seen in the palpal spines of male spiders of the genus *Leptyphantes* and its allies. The most conspicuous of these is the spine on the tibia of the palp of the male *Lepty-*

phantes minutus (Fig. 53). This remarkably thick spine affords the best means of distinguishing this particular spider from its nearest relations, and raises an interesting problem. In one sub-generic group there are four very closely allied species of this genus in which these palpal spines are in each case quite distinctive (Fig. 54). The question, as yet unanswered, arises as to the actual use and significance of these spines, and why should they be so markedly distinct in species so closely related ?

The large spines on the legs are erectile, but their erection does not seem to be under the control of the spider nor to have any special value. It was noticed by Berland in 1912 that, during mating, the leg spines of the spider *Dysdera erythrina* stood out nearly at right angles to the

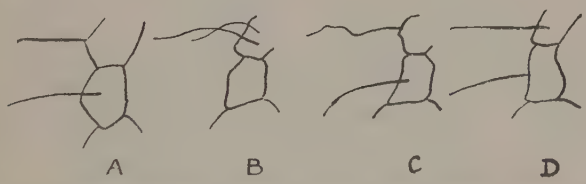


FIG. 54.—Palpal Spines on the Patellar and Tibial Joints of Leptyphantes spp. A, L. minutus. B, L. nebulosus. C, L. leprosus D, L. alacris.

limb and subsided rhythmically to their usual positions as the sperms were discharged. The same thing was recorded by Bristowe in 1922 and by Gerhardt in 1924 for different species, both these authors claiming priority for the observation. It is not a general phenomenon, for in many spiders there is no sign of it. It is probably due to the pressure caused by the flow of the body fluid within, the primary purpose of this flow being the ejaculation of the sperm, and the movement of the leg spines being purely incidental. This interpretation was put forward by Bertkau in 1878, and is supported by the fact that the movement can be induced in a leg detached from a spider long since dead by appropriately squeezing the end with forceps.

The so-called acoustic setae (Figs. 15 and 55) are the

very fine setae situated on the upper surface of the leg-joints, either alone or in a series. In small spiders high magnification is necessary to make them visible at all, and their true function is, to say the least, problematical.

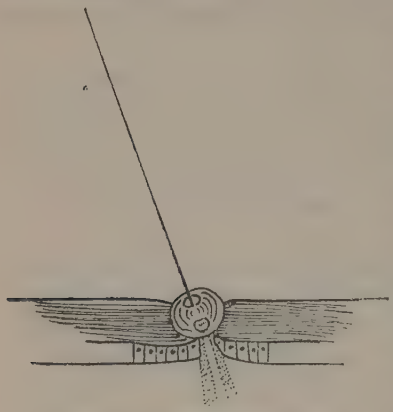


FIG. 55.—An Acoustic Seta. After Dahl.

It is perhaps partly owing to the diversity of these spines or setae and partly to the absence of other definite or easily recognisable sense organs that the spines have been believed in the past to fulfil so many functions. To them have been attributed the functions of protection, feeling, hearing, and smelling—a truly remarkable variety for organs which are, essentially, fairly uniform in structure! No one, however, has as yet suggested that they are *not* organs of touch.

TOUCH

It is to this sense that spiders chiefly trust in their everyday life and all observations of their habits emphasise its extraordinary delicacy. This is especially true of web-inhabiting species, for if a single thread be plucked or a distant corner be touched, the owner of the web, waiting perhaps in the middle or hiding out of sight in its retreat, is immediately aware of the occurrence. The very smallest vibrations of the threads they are holding is appreciable by them, and they can, moreover, distinguish to some degree the nature of the visitor to their webs.

It seems, however, to be rather doubtful whether the sensitiveness of the spider to tactile stimuli is distributed all over the body as uniformly as are its setae. Major Hingston has described the behaviour of a *Hippasa olivacea*

which had lost its palpi. The spider made imperfect webs; it had formerly been able to run on its sheet-web with agility and speed, now it crawled about clumsily, catching its feet in the sheet, tripping up, as it were, and was unable to catch flies. It is well known that the loss of one or even two legs is not a serious handicap to a spider, and this observation would seem to show that the sensations, presumably tactile, conveyed by the palpi, are far more important than those received in greater numbers from the legs.

The discriminating power of this sense is well illustrated by an interesting observation of Bristowe's. A beetle larva was placed in a spider's web, where it wriggled and squirmed in its attempt to escape. The spider came to the mouth of its tube but no further; it would not investigate the cause of the disturbance. After about a quarter of an hour a vibrating tuning-fork was placed beside the kicking larva. The spider immediately rushed out and attacked the fork, which it did not leave until its vibrations had ceased, thus showing that it could distinguish between different types of vibration set up in its web.

Hearing

The problem of the spider's ability to hear is more difficult than that of any other sense, and, since it is connected with the sense of touch, may be considered here.

Very simple experiments with spiders hanging in their webs seem to make it quite evident that they can hear, for they respond to all sorts of sounds by shooting out their forelegs as if reaching towards the origin of the sound. If the first pair of legs are missing, the second pair are held out in the same way, and this response can be elicited by a whistle, a cry, a sounding tuning-fork, a cough or the bark of a dog.

When we recall the many stories which have been told in illustration of the spider's apparent love of music; how they have emerged from their hiding-places at the notes of

a violin; how they have come each night to sit upon a harmonium as often as it was played, and so on, there seems to be good enough reason for believing in their power to hear.

The subject must, however, be considered more fully, more experimentally. In the first place, the spider's reaction to sound is a very curious one, evoked in no other way and quite useless to the spider. If a spider, or any other animal, can hear in the same way as we can, it must be able to interpret the sensation received and to react in an appropriate way. This the spider does not do; its response is valueless.

Moreover, the response is not constant, even within the limits of the same family. The common *Epeira* responds when adult in the way described above, but young individuals of the same species generally drop from their webs at the end of a thread.

Spiders of the closely related genera *Meta* and *Cyclosa*, belonging to this same family, usually drop too in the same way, but *Zilla* scrambles home to its retreat along the free radius, which characterises its web, as quickly as possible.

When we extend our tests to spiders of other families we find contradictory results. All kinds of hunting-spiders are apparently deaf and cannot be made to respond either to tuning-forks or to singing grasshoppers. A negative result of this kind can never be quite satisfactory, especially when dealing with spiders, for spiders show on occasions a stoical indifference to disturbances which do not interest or appeal to them. For example, sometimes a well-fed house-spider will not only pay no attention to a fly kicking about in the web, but will allow the fly to walk up to her, touch her, and even crawl over her without making any movement. The fact, then, that the spider "takes no notice" is not a definite proof that it does not hear, and we must fall back on other tests.

Where, for instance, are the spider's ears? From what has been said above it will be obvious that the setae will be

first suggested, and in 1883 Dr. F. Dahl found that some of them could be made to vibrate in response to the notes of a violin. These setae gained the name of Hörhaare from that date, and the fact that they are sometimes arranged in a graded series made it at least possible that setae of different lengths respond to notes of different pitch. But even so the auditory capabilities of these setae is not proved, and Wagner, in 1888, failing to verify Dahl's results, took exactly the reverse view and insisted that the auditory hairs were only able to perceive sensations of touch. McCook's view, too, was that the sense of hearing is very rudimentary and not really distinguishable from that of touch.

We are thus led to consider the hypothesis that the delicacy of the spider's tactile sense enables it to feel the vibrations of the air which constitute sounds, in somewhat the same way as a deaf person can "hear" the Bourdon stop of an organ. It is possible that its response is a mechanical effect—exactly, in fact, what is implied by the term Barrows suggested in 1915—a positive vibrotaxis. The problem involves principles of resonance, to whose consideration a paragraph may perhaps be justifiably devoted.

Sounds are produced by the periodic vibrations of a solid object communicated to the surrounding air, the main characteristic of the occurrence being the periodicity of the vibrating source. Every producer of sounds has its own natural period of free vibration, dependent on its dimensions, density, and elasticity. This may be likened to the time of swing of a pendulum, which, a simpler problem, depends only on the length of the string. If the weight of the pendulum be suddenly impressed with a force for a very short interval of time, that is to say, if it receive an impulse, it will start to vibrate. Further impulses would increase the amplitude of vibration, or arc through which the weight moves, but, and this is the essential feature of the process, the greatest increase in amplitude will be attained if these impulses are so timed that they recur at intervals equal to the period of free vibration of the

pendulum. Exact multiples or sub-multiples of the period produce a smaller effect, and irregular intervals would produce a smaller effect still. We illustrate our sub-conscious knowledge of this fact when we swing our children in the garden swing and attain an acceptable result with the expenditure of a minimum of effort on our own part. If we did not push periodically we should work much harder and achieve less. It is thus clear that the periodicity of the impulses endows them with the power to produce a cumulative result, as long as the periodicity agrees with that of the vibrating object. An incorrect example of this, due to enthusiastic hyperbole, was the famous suggestion that a boy with a pea-shooter might knock down Westminster Bridge if he but timed his shots suitably.

It should therefore be readily understood that a body may be set in vibration by the incidence of sound waves upon it, if the pitch of the note is the same as that which the free vibration of the body would produce. A familiar instance is the breaking of a glass by a singer's voice. Therefore, it is possible that a spider might be led to respond to sound waves, because resonant vibration might be induced in two situations. The spines themselves might be set in motion, as Dahl observed, or, and this is probably more frequent, the threads of the web may be set a-thrumming. The frequency of vibration of a stretched string is given by the familiar formula, $n = \frac{1}{2l}\sqrt{\frac{T}{m}}$, which shows that n, the frequency, depends on l the length of the string, T its tension, and m its weight per unit of length. All these dimensions will vary in different parts of the spider's web, so that a wide range of possible notes should be able to evoke a response in some part of the web.

If we accept this hypothesis it is easy to understand that spiders may be deaf in the ordinary sense of the word, though they may be stimulated to react to sounds which provoked an answering vibration in either the threads of the web or in their own spines.

Stridulation

The problem may be attacked from quite another point of view—that of the ability of the spider to produce sounds.

Save in a few exceptional cases to be mentioned later, the sound-producing organs of spiders are of the type

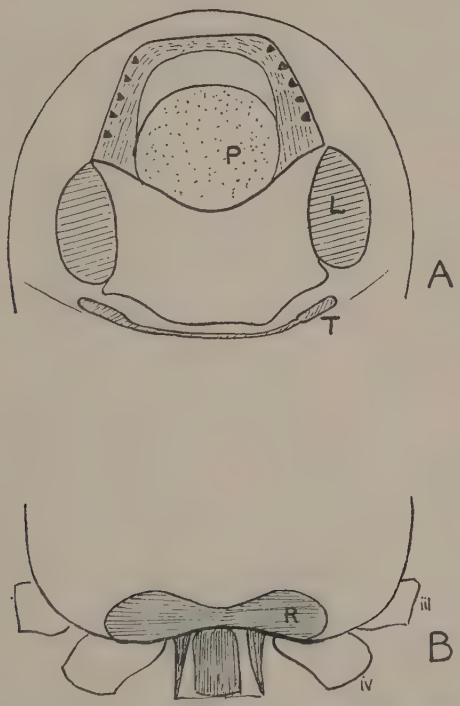


Fig. 56.—Stridulating Apparatus of Steatoda bipunctata. A, Epigastric region of abdomen after removal of cephalothorax. P, scar of pedicle ; L, lung-book ; T, tracheae. B, Cephalothorax from above. R, ridges.

possessed by the grasshopper—that is to say, the sound is made by rubbing two suitable surfaces together. This action is known as stridulation.

The stridulating organs of spiders are diverse in form and situation ; their use remains to some degree a matter

of speculation, for many of them have never been known to produce a sound audible to human ears. Some of them are confined to the male, being absent or rudimentary in the female, and this naturally suggests that they have sometimes a sexual function, and yet there always remains the fact that the majority of spiders exist successfully without them.

Westring, in 1843, was the first to discover a stridulating organ in the spider *Asagena phalerata*. This is a species which may be found in Great Britain and belongs to the family Theridiidae. The abdomen bears just above the pedicle a chitinous collar whose inner surface is finely toothed. The hind end of the cephalothorax is marked with a number of fine transverse ridges over which the teeth scrape as the abdomen is raised and lowered. A very common British spider belonging to the same family, *Steatoda bipunctata*, has a very similar organ, which is borne by the male alone (Fig. 56).

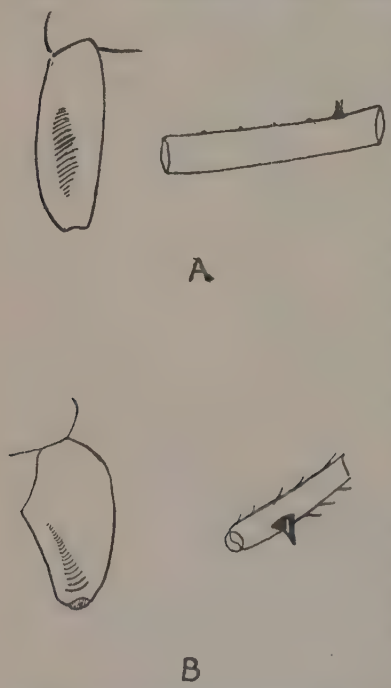


FIG. 57.—Stridulating Organs on Chelicera and Palpal Femur. A, Leptyphantes minutus. B, Scytodes. (B after F. Pickard Cambridge.)

In 1880 Campbell described the stridulating organ present on several spiders belonging to the genus *Leptyphantes* of the family Linyphiidae. This is the family which includes the small black "money-spiders," as well as most of the smallest spiders known. This organ, which is also confined to the male sex, consists of a series of horizontal ridges on the

outer side of the chelicerae, up and down which rubs a small tooth on the femur of the palp. Fig. 57 shows the organ possessed by the common British *Leptyphantes minutus*. Although the movements required to bring these organs into action have several times been seen, no sound has ever been heard. Spiders belonging to the genus *Thomisoides* or *Sicarius*, of the family Sicariidae, found only in the southern hemisphere, can produce an audible sound by means of an organ which closely resembles that of *Leptyphantes*. The sound resembles the buzzing of a bee and is produced by striae on the chelicerae, upon which work a series of teeth on the palpal femur.

This is the most frequent position for stridulating organs, which have since been found

FIG. 58.—Lyra on First Joint of Palp of Psalmopoeus cambridgii. After Pocock.

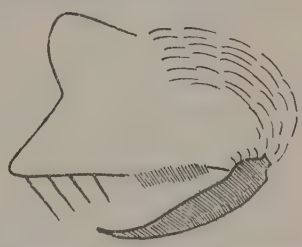


FIG. 59.—Pecten on Chelicera of Psalmopoeus cambridgii. After Pocock.

to be relatively common in the Mygalomorph spiders of the countries between India and New Zealand. These large spiders produce a sound which is audible to our ears, and the first to be discovered was the well-known *Chilobrachys stridulans*. This was heard by Wood Mason in Assam in 1876. He relates how, at work one day in his garden, he was attracted by the sound issuing from something which his gardener was trying to kill with a hoe. It was a large spider which was rescued and taken indoors. Here it repeated the sound when molested by a cat. The spider raises itself on six legs, brandishing its first pair as it emits the sound,

which Wood Mason described as " both peculiar and loud ; it resembles that made by pouring small shot on to a plate from a height of a few inches, or better still by drawing the back of a knife along the edge of a strong comb."

In these Mygalomorph spiders the stridulating organ is possessed by both sexes. The two halves, which may be distinguished as the lyra and pecten, consist of modified setae. The lyra (Fig. 58) is a series of hard, stout rods of chitin, generally club-shaped at the end, but of different lengths and forms. They lie parallel to the surface to which they are attached, generally in a small hollow, designed to receive them. The pecten (Fig. 59) consists of stout spines. The stridulating organs of Mygalomorph spiders are divisible into four types :

(*a*) Lyra on chelicerae, pecten on palpi. This is the commonest arrangement.
(*b*) Lyra on palpi, pecten on chelicerae—the exact reverse of (*a*). This is the type illustrated in Figs. 58 and 59.
(*c*) Pecten on palpi, lyra on coxae of first pair of legs.
(*d*) Pecten on palpi, lyra on trochanters of first pair of legs.

It seems almost certain that in those spiders which possess the organ in both sexes, the sound produced is made with the purpose of frightening enemies, such as the cat and the wielder of the hoe. It might act by warning the hearer of a formidable enemy, better not encountered, or it might, as in the case of *Sicarius*, have the effect of leading the hearer to think that it was made by a bee and not by a spider. The important and obvious fact is that in neither instance is it at all necessary that the sound should be audible to the spider that makes it. Therefore the possession of stridulating powers is not evidence from which the ability to hear may be deduced.

In those spiders, like the Theridiidae and the Linyphiidae, in which the males alone carry the organ, it is necessary either to postulate an ability on the part of the

female to hear the sound, or to assume that the vibrations produced in stridulating are transmitted as such along the threads of the web, and that the female feels them in the ordinary way. This is at least probable and enables us to retain our belief that the spider is really deaf.

However this may be, there is no doubt that the power to stridulate has proved of value, for it has been evolved in so many different groups of spiders. In addition to the types of organ already mentioned, at least three others are known and are of interest because they occupy different positions on the body. This would tend to show that the various types of stridulating spiders have acquired the power quite independently and therefore do not always possess the organ in the same place.

In *Selenogyrus*, a trap-door spider from West Africa, the action is between two small rods, one on the inner surface of each of the chelicerae. This type, discovered by Hirst in 1908, is unique in that the two halves are alike.

In *Cambridgea antipodiana*, a spider belonging to the same family, Agelenidae, as our house-spiders, there is a hollow in the front of the abdomen lined with six shining black arches of hard chitin. Upon these plays a heart-shaped tooth borne by the hinder end of the cephalothorax and projecting into the hollow. This was discovered by Pocock in 1895 when examining the preserved male spider in the British Museum, and thus no occasion of its use has been described.

Finally, perhaps the most remarkable of all, is the stridulating organ possessed by the very small British Linyphiid spiders, *Entelecara broccha* and *Eboria caliginosa*. In these it is confined to the male sex. Each lung-book is protected by a chitinous cover or operculum (Fig. 60) with a roughed surface, and on this surface scrapes a sharp tooth-like projection on the inner side of the fourth coxa. There are thus at least eight or nine distinct types of stridulating organs known.

In addition, by at least three known methods spiders have been heard to produce sounds. In Staten Island the

wolf-spider, *Lycosa kochii*, is known as the purring spider from its habit of drumming with its palpi on the dead leaves over which it runs. It runs about and stops at intervals to purr. Many other members of the same family perform the same action when excited by the presence of a female, but no sound has been heard from them. Prell has lately investigated the habit, which, he concludes, makes it easier for the two sexes to find each other. He

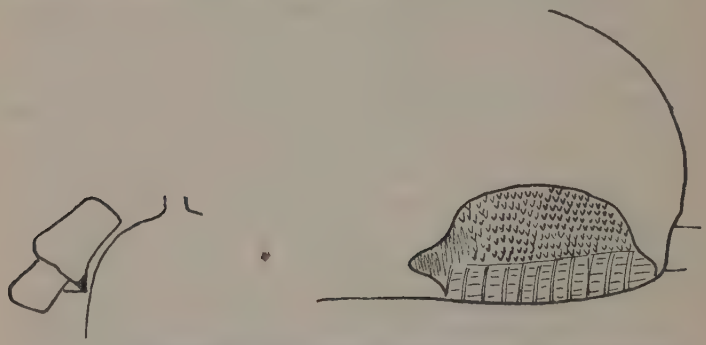


FIG. 60.—Stridulating apparatus of Entelecara broccha between fourth coxa and lung-book. After Falconer.

has been able to imitate the sound or the vibration or both with a wet file, and has observed that the spiders upon which he was experimenting would only look for each other while his artificial notes were sounding.

Bristowe has recorded the production of sound by another wolf-spider, *Tarentula pulverulenta*, as its pulsating abdomen strikes the ground, and also by a jumping-spider, *Euophrys frontalis*, on raising its legs and lowering them so that the tips of the second pair hit the ground.

SCENT

While there is no doubt that spiders can smell, there is considerable difficulty in determining the nature and situation of the structures concerned.

Dr. and Mrs. Peckham investigated the response of spiders to the scent of various essential oils as long ago as

1887. They were careful to use no substance which could have an irritant effect, and simply presented to the spider first a clean glass rod and then the rod dipped in the scented liquid. They found that web-spiders responded by raising their legs, while hunting-spiders gave evidence of their being aware of the odour by leaping upon the rod.

More extensive experiments were made by Pritchett in 1905. Her spiders were confined in triangular cages with mosquito-netting for bottom, and scented glass rods were brought under them as they stood in the cage. The smells of many different sorts of liquid caused spiders to respond by vibrating their palpi and by raising their legs. The loss of various legs did not impair the spider's power to respond. Dahl's suggestion that some of the leg spines are organs of scent was tested by cutting off all the spines of one spider and then sand-papering its legs smooth. The response to smells was not affected by this treatment, and the conclusion drawn was that spiders possess a good sense of smell and that the spines are not the scent organs, which must be scattered over the body.

It was at this point that the mysterious lyriform organs were suggested as possible organs of smell, and these must now be described.

If the legs of spiders are carefully examined with a microscope, there will be found in certain situations, generally near the ends of the joints, darkish patches which seem to consist outwardly of ridges in the smooth chitin. These are the lyriform organs. They are present in all spiders, in Opiliones (harvestmen), and false-scorpions, but absent from mites, scorpions, and solpugids. Their positions in spiders are remarkably constant, and Gaubert gave in 1890 the following table, indicating the occurrence of sixty-eight such organs on the legs and palpi.

	Joint 1.	Joint 2.	Joint 3.	Joint 4.	Joint 5.	Joint 6.
Palp . .	1	1	2	—	—	—
Leg 1 . .	—	1	1	3	3	1
Leg 2 . .	—	1	1	3	3	1
Leg 3 . .	—	2	1	1	1	1
Leg 4 . .	—	2	1	1	1	1

In addition there are thirteen lyriform organs on the cephalothorax, sixteen on the sternum, and some on the chelicerae and abdomen. Their situations and structure,

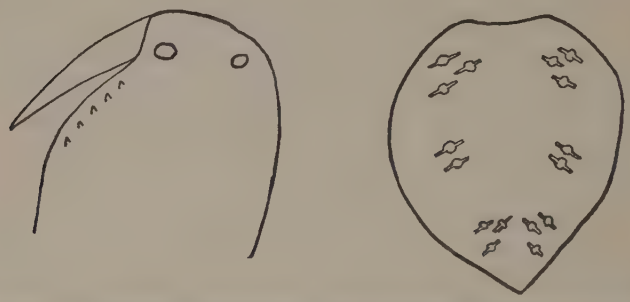


FIG. 61.—Diagrams showing the positions of the lyriform organs on the chelicerae and sternum. After Gaubert.

shown in Figs. 61 and 62, have long been familiar, and it was at first believed that they were auditory organs. Gaubert denied their auditory function ; he tried the effect of varnishing the organs and found as a result that the

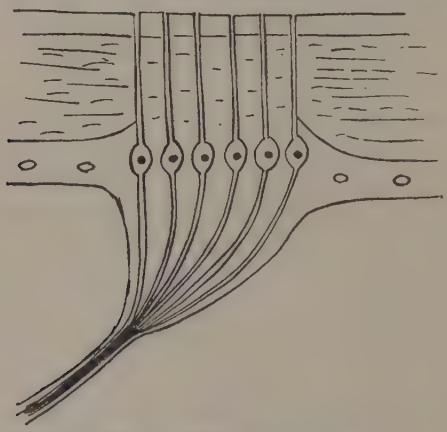


FIG. 62.—A Lyriform Organ. Diagrammatic section, after Gaubert.

spider was less sensitive to heat. He believed that their structure bore out his hypothesis that they were perceptors of heat, yet in his conclusion admitted that they

might receive "peut-être aussi d'autres sensations générales."

These are the organs to which appeal has been made to support the contention that spiders have scent organs in various situations. The idea is based chiefly on the work of Prichett supported in 1911 by further investigations of McIndoo. After obtaining the usual response to smells, McIndoo endeavoured to cover the lyriform organs with a coat of vaseline. He then found that the time of response to smells was very much increased, and so concluded that the lyriform organs were organs of scent.

An alternative view was, however, put forward in 1916 by Hewitt. His subject was a Mygalomorph spider belonging to the genus *Stasimopus*, and he presented the scent to it on a hat-pin. This, being much finer than a glass rod, enabled the experimenter to make a more exact localisation of the stimulus, and hence a more accurate discernment of the positions of the scent organs. Hewitt's experiments showed that a scent placed near the tip of a leg resulted in that leg being raised and moved away, but if the leg was amputated at the centre of the penultimate joint, the metatarsus, it did not respond at all. This points to the concentration of the scent organs near the tips of the legs, rather than to their scattering over the body, and Hewitt suggested that they were localised in the scopula hairs. He also showed, as his predecessors had done, that the first and second pairs of legs are more sensitive than the posterior pairs, and that males are better endowed with smelling power than females. It will be seen that if the scent organs are either the scopula hairs themselves, or are situated in their immediate neighbourhood, the lyriform organs are left without a recognisable function and remain a problem. This is indeed the view held by Vogal as recently as 1922.

Finally, we come to Bristowe's recent observations on courtship in wolf-spiders, in which he showed quite conclusively that the male wolf-spider recognises the presence of the female by smell. Further, the male can follow the

track of the female and can be seen excitedly feeling the ground over which she has passed with the upper surface of his palpi and the tips of his legs. This tends to support the view that the scent organs are placed near the tips of the tarsi. In an experiment of Bristowe's the tips of the palps and of the tarsi were removed from a male spider under chloroform. In twenty-four hours it had apparently recovered, and fed on a fly. It responded, however, very feebly to a scented hat-pin and seemed quite unable to recognise the scent of a female.

The lyriform organs are not glandular and it seems certain that they are sensory. Bristowe makes the suggestion that they are indeed organs of scent, used, like the scent organs of some male moths, for recognising smells at a distance. When, however, the origin of the smell is close at hand, as, for instance, in following a track on the ground, the hypothetical tarsal organs are used.

The value of Bristowe's work is that it indicates for the first time what advantage a sense of smell may be to the individual spider. Scent is not used to any extent in catching food. This was proved by Rainbow, in his experiments already mentioned, when he found that spiders would leap upon rude imitation insects dragged into their range of vision.

Taste

It is well known that the sense of taste and smell are related, at any rate in man. No further reminder is needed than the monotonous insipidity that all food acquires when we suffer from a cold.

The tasting ability of spiders is not a subject that has been much investigated, and on *a priori* grounds it would not seem that they possessed the sense to any great extent. It seems that spiders do not select their food but are willing to accept all that comes their way, and if it be the normal behaviour of a creature to eat everything that becomes available without discrimination, the sense of taste is not to be expected. Moreover, Boys, many years ago, tried the

experiment of drowning a fly in paraffin oil and throwing it into a spider's web. By touching the fly with a tuning-fork, the spider was made to come out and attack it, and by repeating the process was induced to eat a large portion of the fly, paraffin and all.

On the other hand, some facts point to the reverse conclusion. The most familiar is contained in Fabre's description of an *Agelena labyrinthica* which he fed on locusts. "The bite," he says, "is usually given at the lower end of a haunch: not that this part is more vulnerable than any other thin-skinned part, but probably because it has a better flavour. The different webs which I inspect to study the food in the larder show me, among other joints, various flies and small butterflies and carcasses of almost untouched locusts, all deprived of their hind legs, or at least of one."

It is, therefore, also of interest to see occasionally a house-spider pick up detached legs and suck them, as if they were, as Fabre suggests, "a dainty, the equivalent on a very small scale, of the larger legs of the crayfish."

A recent experiment of Hingston's may also be cited. He chose quinine as a substance possessing no smell and no irritant action, and tried the effect of feeding a spider on a fly soaked in quinine. The spider came out and bit the fly, after which it returned to its resting-place and vigorously brushed its palpi over its maxillae. This action, coupled with its immediate rejection of the fly, seems to prove that it was well aware of the quinine, and it is difficult to imagine that anything other than the taste was concerned.

CHAPTER V

THE BEHAVIOUR OF SPIDERS

We have described the spider's body in some detail, analysing it into systems and organs and cells and synthesising it as an organised unit capable of response to changes in its environment, and in so doing we have looked upon the organism from one aspect only. A second remains, for every living creature is properly to be regarded as a dual entity—a physical body and a psychical mind. What can we learn about the spider's mind—the subtle inner power that sits in control of the cells, the organs, the systems ?

We are ignorant of the true nature of the connection between the mind and the body : that is to say, we do not know what difference, if any, in the cells of the nervous system is responsible for the passage of a thought, the perceiving of an impression, the creation of an idea. The interpretation of the animal's actions as they reveal the character of the controlling mind within is as far as we are able to go, at present.

It is clear enough that the diverse types of animal behaviour are of different degrees of complexity, even as are the diverse types of animals' bodies. Structure, not behaviour, reveals evolution as a racial history of the body, and similarly behaviour, not structure, reveals the history of mind. So we come to perceive an evolution of mind comparable and perhaps contemporary with evolution of body. Therefore we ought to look upon the mental and the physical as two allied aspects of the life of the organism. Perhaps they are only two ways of looking at the same thing.

Reflex Actions

The simplest type of behaviour which the spider well illustrates is the reflex action. We ourselves blink at a sudden appearance near the eye, we draw back our hand from too hot a surface : these are reflex actions. We are conscious of them, but they are involuntary. They depend on well-established connection between certain nerves and certain muscles and are performed without our " stopping to think."

The spider's most frequent reflex is its habit of " shamming dead," as it is generally and inaccurately termed. The spider draws up its legs and remains absolutely motionless in a cataleptic condition. The habit is general in all families of spiders and is the usual response to a threat of danger such as a sudden jarring of its surroundings. Thus a spider in a box may be made to assume the position by a tap on the lid. Experiment has shown that this action is carried out perfectly by spiders whose abdomen has been completely severed at the pedicle. We are reminded of the familiar automatic actions of the headless frog. Moreover, in some cases it was found that if the spider was again bisected, so that each half of the cephalothorax carried two pairs of legs, the two halves still retained the power to respond to a neighbouring tap. The withdrawal of the legs was slower, but the same power was at work.

Sometimes a reflex action involves more than this. We rise a step in the ladder of behaviour when we come to such compound reflex actions as demand the co-operation of several parts of the body. When, for example, the cataleptic reflex is called forth in the web-spider, when, as we say, " the web-spider is frightened into shamming dead," it simultaneously drops from its web. But it does so on a thread, and the silk glands must co-operate in the action and in the checking of the stream of silk after a certain fall. Other web-spiders re-act in another way, very familiarly shown by the common garden spider. They shake their webs into rapid vibrations by rigorous rhythmical jerks of their legs. This demands suitable co-operation of all the

leg muscles and a proper timing of their contractions. There is more in this than in mere quiescence, but it is still a reflex action, an automatic response under the control of a part of the central nervous system which is not concerned in volition.

To describe the performer of any of these actions as cunning is an anthropomorphism quite unjustified by the facts, and nowadays is less commonly heard. It is the rule of behaviourists to interpret the actions they witness in the simplest possible terms—to credit the animal with a minimum degree of mentality. A stage will certainly be reached at last when the creature's behaviour cannot be properly described without the use of psychological terms. It must then be admitted that the animal is showing something akin to conscious judgment, and the psychological aspect is dominant over the physiological. Before this was realised, the habits of animals were often described in the most extravagant terms. Most popular Natural Histories of the eighteenth and nineteenth centuries will afford examples, but none is better than Evelyn's oft-quoted description, in his *Travels in Italy*, of jumping-spiders. "I have beheld them instructing the young ones how to hunt, which they would sometimes discipline for not well observing; but when any of the old ones did, as sometimes, miss a leap, they would run out of the field and hide themselves in their crannies, as ashamed, and haply not to be seen abroad for four or five hours after."

Tropisms

Tropisms are allied to compound reflexes, but differ in two respects. They generally involve movements of the whole body rather than of a part, and they are generally due to an automatic adjustment of the body so that the stimulating impulse is received equally by both sides. The most familiar examples are the flight of the moth to the light and the tendency that young eels show to swim persistently upstream.

Spiders show at least two well-defined tropisms. In youth they are negatively geotropic and tend to climb upwards; and at all ages they are usually negatively heliotropic, tending to move away from bright light.

The geotropism of the young spider is associated with the method of dispersal in which it floats away on a gossamer thread. When once the flight has been made and the dispersal effected, the tropism fades away from the spider's constitution. In one of Fabre's experiments, a cocoon of the eggs of the garden spider, *Epeira diademata*, was allowed to hatch at the bottom of a fifteen-foot bamboo. When the young spiders hatched they began to mount. They climbed only at certain hours in the day and spent the night resting together in their customary globular formation under a cone of silk. And so they climbed on until after four days they reached the top of the bamboo and none ever turned to come down again.

Young wolf-spiders, even though their whole adult life is spent running on the ground, will show the same propensity. They will climb once as high as possible, and thereafter no more.

That spiders tend to shun the light is perhaps the first characteristic that any observer would notice. Indeed, it is possible that their apparent preference for red may be a result of this tropism rather than of any real appreciation of colour, and some experiments might well be devised to test this. There is, however, one particularly good example of the light-shunning habit. On the beach at Wood's Holl, Massachusetts, a little spider, *Grammonota inornata*, is found, hiding under clumps of eel-grass. On lifting a clump of the grass when the sun is shining from any point in the sky save directly overhead, all the disturbed spiders run landwards. This universal choice of the same direction is not affected by the slope of the sand, for they will run uphill or down, nor by the presence of water, for they will run over it, nor by the direction of the wind. But if the grass-clumps are lifted at midday, or in sunless weather, or at any time under the shade of an umbrella, the spiders will scatter

indiscriminately in all directions. Montgomery, who described this curious phenomenon and carried out laboratory tests on the tropisms of the spiders, explains it as a running away from the glare of light reflected from the surface of the sea—in fact as negative heliotropism.

There are, of course, some spiders which do not so generally shun the light. Many wolf-spiders, which are seen in immense numbers in the sunshine, have an incredible way of disappearing altogether if the sun is temporarily obscured by a cloud.

It is possible, too, that the orb-spider's response to the shaking produced by the entangled fly at one spot in its web is an action of this type. This vibrotaxis was investigated by Barrois by shaking one spot of the web with an electrically-driven oscillator and photographing spider and web by a timed flashlight. The photographs revealed both the speed of the spider's response and also the distribution of the vibration along the threads of the web. This made it clear that the spider was being directed to the centre of disturbance, as it were mechanically. A few simple experiments in blowing a puff of air on to the web soon lead one to the same conclusion. There is no need for the sight of an insect nor the sound of its wings nor the continuance of its struggles to make the spider dart out.

Simple Instincts

On a plane above these reflex and tropistic responses come the many actions which we ascribe to instinct. Instinctive actions are distinguished by two important characteristics—the fact that they are carried out perfectly on their first performance without previous learning, even though they are often of considerable complexity, and the fact that they must be initiated by some particular stimulus. In this latter aspect they recall what we have previously said about reflexes, but differ in this—that each of the successive actions would seem to be set in train by its predecessor and not by a succession of external stimuli. Further, the

psychological aspect is more prominent in instinctive behaviour than in reflex actions. There is a degree of consciousness or awareness about instinctive actions which not only enables them to make a contribution to experience, but which, as a result of this, also makes it sometimes possible for individual experience to modify the instinctive actions themselves.

It is clear, however, that instinctive behaviour depends on the inherited structure of the nervous system; in no other way could learning be dispensed with and the linked semi-reflex actions follow one another to completion. Nor from any other source could there arise that imperious coercion which often drives the animal through a long series of instinctive actions when an accident or an alteration of circumstance has made those actions useless.

Instinctive behaviour is well developed in spiders and includes the majority of their activities; it is therefore not difficult to select some which illustrate the chief features mentioned above. Probably the most obvious of all is the ability of the young spider to spin its own web as soon as it begins to lead an independent life—a web which follows in every respect the design of the webs of the adults and is just as well adapted to its purpose. The achievement of spinning a web is more complicated than is the swimming of a young bird, and yet no parental instruction is given to the spiderling, as it sometimes is to the bird. In the majority of cases the parent is long since dead.

The behaviour of spiders illustrates the modification of instinctive actions in special conditions much less frequently than the contrary fact of their tyranny, but the following is perhaps an example. Major Hingston, watching an orb-spider spinning the radii of its web, tried the experiment of cutting a radius as soon as it was laid down. Twenty-five times the spider replaced the missing radius before it gave up and altered the usual plan of its web, spinning one with eighteen radii. To obtain these eighteen it had had to spin twenty-five extra radii, making a total of forty-three instead of the usual twenty-four.

But as we have said, instinctive behaviour in spiders remains in most cases unmodified. The house-spider, for example, usually coats its egg-cocoon with a layer of small pieces of brick-dust and grit which have the effect of making it far less conspicuous and probably also more resistant to the attacks of parasites than it would otherwise be. But a spider in a cage makes its cocoon conspicuous by gluing to it the wings and legs of dead flies, which would not protect it at all.

Similarly, when Moggridge removed from the neighbourhood of trap-door spiders' tubes the moss with which they generally coated their doors and scattered about pieces of bright wool, the door was coated with the wool and made conspicuous instead of invisible.

The wolf-spider, *Lycosa narbonnensis*, is one of the few European members of its family which lives in a permanent home—a burrow excavated by itself. But Fabre showed that if it was taken away from the burrow which it had dug, it showed neither inclination nor ability to dig another. Its instinct impelled it to dig a hole and to live in it, but was not prepared to cope with a situation so altered that a succession of holes might be necessary. So the spider went homeless, but showed itself wise enough at least to take possession of a hole made for it by pushing a pencil into the soil.

It is evident that no very great degree of consciousness lies behind these straight-forward instinctive actions; otherwise their modification in special circumstances would be less rare. When an animal modifies its behaviour in accordance with circumstances—that is to say, when it appears to be profiting from its past experience—it is providing us with all the evidence we have that the past experience was indeed a conscious one. The house-spider, making its sheet-like cob-web, shows no sign of profiting by experience. It never spins more rapidly nor more wisely nor more efficiently: it never improves. Previous experiences of web-making and of the hazards of the chase have taught it nothing, and we are scarcely sure that it actually knew that

it was spinning. There is not, as Romanes has long since pointed out, "any necessary knowledge of the relation between the means employed and the end attained." Thus we can understand, perhaps, the apparently absurd way in which spiders will spin their webs in sealed museum cases, or even in small cages. They do not spin until they have discovered that they cannot escape, but it is too much for them to realise that this means that insects cannot fly in. So they spin—instinctively, irresistibly, irrationally.

Chain-Instincts

Proceeding, we may find instinctive actions which are so complex, so prolonged, and so dependent one upon another as to deserve consideration as a higher stage of behaviour. These are termed chain-instincts.

In the example last quoted, the spinning of the house-spider, the cob-web is made almost entirely of one kind of silk and by one kind of action. But the geometrical web of the orb-spider is, as will be seen in a later chapter, a more elaborate work. It consists of at least five parts made by methods and of materials so different that a Labour newspaper has commented on the fact that, if spiders were trade unionists, five spiders would be required to spin each web. The extended series of processes by which it is made thus form a good example of what is meant by chain-instincts—a succession of different instinctive actions forming integral parts of a unified performance.

Every spider provides an illustration of chain-instincts in the making of its cocoon, a process which, as will be described later, consists of several different stages. The finished cocoon, often so beautiful and elaborate an object, is produced by an unvarying succession of processes, initiated by the internal stimulus of the matured ovary. Probably also the courtship actions of male spiders are to some extent similar in character. Instigated by the sight or scent of a female, the male carries out a series of peculiar rhythmical movements, different for each different species.

These chain-instincts serve to emphasise most strongly the way in which an instinct drives the animal through its task with very little chance of altering the procedure. The egg-cocoon once begun is finished, even if the eggs are taken away or have fallen to the ground. This fact has often been spoken of as remarkable, but it is what might be expected from the nature of the case, and it is misleading to use it as an instance of the spider's stupidity. The spider cannot know what eggs feel like or look like, and therefore cannot realise either their absence from the sheet or their presence on the floor of the cage. In the same way a male spider can be persuaded to go through his initial courtship antics without a female being present at all, simply by putting him in a cage which she has lately occupied and in which her scent still lingers.

But web-spinning is by far the best illustration of the tyrannical character of instinctive actions, because it lends itself well to such a variety of experiment. Fabre was the first to describe the effect of cutting the orb-web in half as soon as it was made. The spider remained on the tattered and useless wreck, and showed no inclination to make another. This was repeated by Hingston, who made many other experiments of a similar character. For example, if a piece of the temporary spiral line which the spider uses as a scaffolding is cut, the spider does not replace it. Each time that it comes to the place as it circles round the web, it has to make a longer journey because of the missing thread, but it will do so invariably. It cannot break off a process in the middle and go back for a moment to a point earlier in its course. In an extreme case, Hingston removed the whole of the scaffolding. This meant that as the spider laid down the viscid spiral thread it had to travel from the edge to the centre and back again in each segment of the web, instead of merely stepping from radius to radius with the help of the scaffold. And yet the spider did this and spun, in this laborious way, a crude and imperfect web, instead of re-laying the few turns of scaffold.

As an alternative, the radial threads were removed. This

destroyed the balance and symmetry of the system, but the spider took no notice. Even when seven radii were removed, it still spun on as best it could.

In a most illuminating experiment, Hingston removed the first ten turns of the viscid spiral thread. The spider, alarmed, retired to its hiding-place, but, some time after, came back to the web, where all was quiet. And there it began at the place where it had left off, and put down the second half of the viscid spiral. It could not go back and start this thread again; it could only go blindly on.

It is important to look upon these facts rather as illustrating the character of instinctive behaviour than as affording grounds for criticising an animal's abilities. An animal has as much mental endowment as it wants, and no more; or, to put it another way, an animal's habits are adapted to the limits of its mental capacity. In the life of the spider, the chain-instincts are capable of carrying on the spider's essential businesses and securing its survival. They do so in a very efficient and, it must be admitted, a very successful, way without waste of time or energy. We must not in any way condemn the spider for a fool as a result of our experiments. Nature does not play tricks like ours; she does not steal spider's eggs nor tease them with scents nor juggle with webs in the making. At her worst she makes a hole in the web as soon as it is finished. And so we do not and should not expect to find a mental equipment designed to cope with situations which are unlikely to arise.

This is illustrated by this very question of repair. It has been seen that a bisected web is not replaced; in the same way, if we push a finger through the web, the spider cannot mend the hole. But when, in the natural course of events, the spider itself tears a large and struggling fly from its toils, it almost invariably puts down a few threads, which support the web as a whole by preventing the rent from getting worse. Warren has noticed the same power in *Palystes natalius*, a Natal hunting-spider. Many of these laid eggs and spun cocoons in his laboratory and, if the egg-

sacs were injured, the mothers made attempts to repair them, with varying degrees of success.

Behind all instinctive actions there is a feeble awareness and a faint endeavour.

Intelligence

The last of our stages of spider behaviour gives us a glimpse of intelligence. Mere associative learning passes on to experimental learning ; there is a conscious adaptation of means to an end which implies the possession of some degree of memory and imagination.

Intelligent behaviour in the true sense is very rare among Arachnida. It has been seen that instinctive behaviour suffices for most of their needs : they are pre-eminently creatures of the instinctive type. Animals of this type, reaching a climax in bees and ants, are possessors of small brains, but are inheritors of fully developed instinctive powers. They are adapted to a constant environment and are difficult to educate. On the other hand, birds and mammals represent the big-brained type. They inherit a relatively small endowment of instinctive behaviour, but they stand a far better chance of survival in a world of shifting scenes and problems, for they possess the power to learn, and to learn intelligently.

Like almost all other creatures, spiders can learn by association. When they are kept in cages, for example, they will at first always retreat when the cage is opened to put in the flies on which they are fed. As time goes on the speed of their retreat grows less, and at last it is very difficult to believe that the expectant spider within does not associate the opening of the cage with food.

That spiders can so far be " tamed," as we say, as to take a fly from one's fingers is only a further example of the same power. That they will ultimately refrain from running out to a tuning fork that is used to shake their webs is another.

For learning of any sort to be valuable, a memory is necessary. The spider's memory is usually short, and there-

fore it learns very slowly. Dr. and Mrs. Peckham tried to teach a *Cyclosa conica* that it need not drop from its web at the sound of a tuning fork, for no harm resulted. The spider was tested with the fork daily and for a month it dropped at every sound. For another fortnight it dropped six or seven times daily before "remembering," and at last after six weeks, it remained unmoved by the sound.

Probably the highest exhibition of the spider's intelligence is seen when it has caught a large and heavy insect. It poisons it and ties it up by actions which are undoubtedly instinctive, but before it enjoys its meal it has to raise the captive to its own retreat. One may watch small orb-spiders thus dealing with crane-flies.

The conditions of the problem before the spider are bound to vary. The insect may be firmly stuck to the viscid spiral, or not; it may catch the wind, or not; and so on. Yet the spider goes busily on, fixing threads and cutting threads, every action apparently well-chosen and directed towards the same end. The fly is raised stage by stage, first one end and then the other, as if an intelligent foreman were calling out directions all the time.

Probably the spider is doing little more than experimenting. It fixes some threads and then pulls up the fly and repeats the process if necessary. But here, more than elsewhere, the spider shows ability to deal with uncertain problems.

CHAPTER VI

THE QUEST FOR FOOD

It is common knowledge that spiders are normally insect-eaters and that they spread their webs and direct their energies to catching flies. The closest study of spiders can but modify this by amplification, for web-spiders are usually ready to eat everything that shakes their web and the hunters will attack anything small enough that comes their way, without pausing to determine whether or no it has six legs and a head separated from its thorax. Instead of describing them as insectivorous, it is therefore a little more accurate to say that they are carnivorous and eat only living food.

The Choice of Food

The spider's wide choice of acceptable fare has already been referred to in discussing its sense of taste. Experience shows that spiders will eat all kinds of flies as well as wasps, bees, ants, beetles, earwigs, butterflies, moths, harvestmen, and woodlice, and other spiders, whenever opportunity occurs. More rarely they have been known to consume caterpillars and pupae, worms and small fish ; they show no trace of discrimination. Abraham (1924) has, however, recorded of a captive *Cryptothele sundaica* that in five months it could not be induced to eat anything except termites.

This varied menu should not be interpreted as a suggestion that the spider unhesitatingly rushes at everything which entangles itself in its web. In the first place, the actual vibration conveys a certain amount of information.

An instance of the spider's treatment of a struggling beetle larva as being unworthy of its attention has already been given, and the female spider is also able to distinguish the tune played by a male spider when he comes a-courting on the edge of the web.

On occasions, too, the web entraps formidable insects with stings, like wasps, or with powerful jaws, like the praying mantis. The spider has then to determine whether to allow the struggling insect to force its way out of the web, or whether to attack it by special methods. The ordinary large English house-spider, *Tegenaria atrica*, will generally allow a wasp to escape, and I have seen one to whom the wasp in its struggles had approached too near, hurriedly bite a hole in the sheet of the web and, evidently frightened, force its way through into a less dangerous neighbourhood. On the other hand, many a hungry house-spider attacks and overcomes wasps. The method by which they do so, as well as the possibility that sight may help the spider to distinguish between its welcome and its undesirable captures, is suggested by an observation of Pocock's on a spider, *Agelena labyrinthica*, belonging to the house-spider's family. The *Agelena's* web had entangled a bee, of whose sting the spider was evidently afraid. It therefore attached a thread to a point near the bee and walked round and round it so that the thread hampered the insect's movements. Then quickly it darted in and bit the bee in the leg. As soon as this had been accomplished, the character of its actions entirely changed. It seemed to worry no more about the possibility of the bee's escape, trusting in the effects of the poison, which, in fact, soon paralysed the bee.

It is evident that sight played its part in determining the spider's course of action, for it would unhesitatingly bite a bluebottle as large as the bee and carry it into the corner at once. However, when given a drone fly, *Eristalis*, it treated it in the same way as it had treated the bee. Clearly it mistook it for a humble-bee, even as a man might do. Campbell recorded an observation which points in the same

direction: he was keeping a house-spider in a bottle and says that when searching for flies she could be seen to tilt her whole body as if making the best use of her eyesight.

The Treatment of Captives

Pocock's observations on the actions of *Agelena* illustrate what may be called the direct and indirect methods by which the web-spider deals with its captures. If the insects are not too large or are well entangled, or if they are quite powerless to harm the spider, the latter hurries to the scene as soon as they arrive, seizes them and drags them home to be eaten. The indirect method is used when the booty is formidable and likely to hurt the spider, or when it is so strong that its continued struggles might tear undesirably large holes in the web and allow it to escape.

The common garden-spider, *Epeira diademata*, shows the most familiar of these methods of treatment. The fly is grasped with the first and second pairs of legs and turned round with the help of the third legs and the palpi, while the tarsal joints of the fourth legs guide the broad ribbon of silk which is issuing from the spinnerets.

The house-spider, *Tegenaria*, uses an interesting modification of this plan which achieves the same result. It holds the captive with its jaws and, pressing it down into the sheet of the web, walks round it and so twists it up in sufficient silk to keep it quiet.

The method of drawing a thread round the struggling victim, used by *Agelena*, has already been mentioned, and there are still some others.

Our holly bushes often carry in the summer months the webs of spiders of the genus *Theridion*, webs which consist merely of a maze of threads crossing in all directions. The spiders of this family have been mentioned in Chapter II as the possessors of a comb of spines on the tarsal joints of the legs of the fourth pair. These combs draw out silk bands from the spinnerets and throw these ribbons and sheets of silk over the captive. This is so effective a method of

encumbering the insect's limbs that these small and comparatively weak spiders are able to overcome insects much larger and stronger than themselves.

Another type of web which is very familiar in all our gardens is the flat sheet type, the spider living beneath it, hanging and running upside down. When it arrives at an entangled insect, it usually bites it and pulls it through the sheet at once, but I have also seen the spider stop beneath a struggling insect and pluck at the sheet with a sharp jerk so as to entangle the insect further.

This plucking at the web is a common action of many spiders when their web has been shaken by a single isolated twinge. Such a twinge may mean either that the insect merely brushed the web in passing and so has escaped, or, as is frequently the case, that it has been caught and is lying still. The pluck at the lines of the web tells the spider whether the threads are loaded or not and also stimulates the insect, when there is one, to further struggles, which entangle it more securely. Garden-spiders can often be seen turning about in their webs and testing their luck in this way, while house-spiders gently withdraw their fore-legs, which pull on the sheet, so that one can see the little cones of silk pulled up by their claws.

Specialised Webs

There are, moreover, many kinds of specialised webs, whose use is more intricate than that of the simple wait-and-see type.

Probably the best-known of these is the sectoral web of *Hyptiotes*, the triangle-spider. The web of this spider is best compared to three sectors of an orb-web with a silk thread attached to the apex (Fig. 63). At the other end of this thread the spider waits hidden under a leaf, the thread hauled in and coiled up by its forelegs. If an insect flies into the web, the spider lets the thread go, jerking the triangle of web.

Two of the most remarkable methods of using webs

have been described by Dr. Conrad Akerman, of Pietermaritzburg.

Near the south coast of Natal, a fairly large spider,

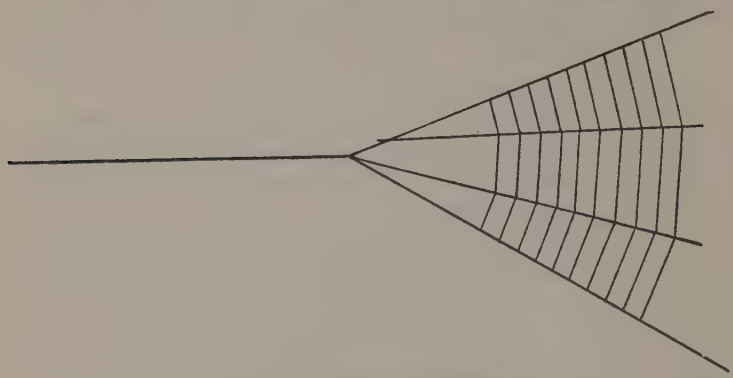


FIG. 63.—Web of Hyptiotes.

Menneus camelus, spins its webs on bushes in the neighbourhood of streams. The web (Fig. 64) consists of a few irregularly placed threads supporting a band of about twenty threads of silk. These are adhesive, being covered with the loops of the viscid silk produced by the cribellum, the supernumerary spinning - organ already described. This little band, scarcely bigger than a postage stamp, seems at first sight far too small to catch anything. But that view disappears when the method of using it is discovered. The spider stands close beside it with its four front legs holding the corners of the band. If a moth approaches, the spider suddenly stretches the web until it is five or six times its former size and simultaneously hurls itself

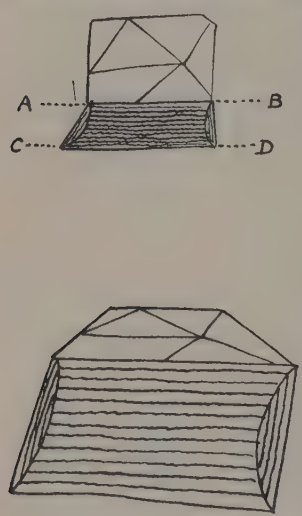


FIG. 64.—Expanding web of Menneus camelus. The points A, B, C, and D are held in the anterior tarsi.

forward. The web is thrown round the moth and closed with the forelegs; the moth is helpless in the sticky toils and the spider at once bites it. The principle is exactly the same as that of the old-fashioned butterfly-net, which was used with two hands and folded over the butterfly. The spider does not always succeed in catching the moth: it may lose its grasp of the web, which is sometimes damaged by the twigs. But the spider picks it up again carefully by the four corners, tests it to see if it is working and resumes her vigilance. She never makes a second net in the same evening, but continues to use the same one, however damaged it may become.

An even more striking method is that adopted by the spider *Cladomelea akermani*. This is a large Epeirid spider, 15 mm. long, with 24 pointed tubercles on its abdomen. It does not seem to spin a web; instead it drops a single thread about 2 cms. long, having at the end a globule of viscid matter a little larger than the head of an ordinary pin. It holds this thread with one of its shortest legs—the third pair—and whirls it rapidly round in a horizontal plane. This is continued for about a quarter of an hour without stopping; then the spider draws up the thread and swallows the globule. After a few minutes' rest another line and globule is spun and the process repeated for another fifteen minutes. This may continue for several hours. If any insect were to come within the radius of the spinning drop, it would probably be struck by the line and captured.

In Australia there is a spider, *Dicrostichus magnificus*, related to *Cladomelea*, which spins a similar thread and droplet. It does not twirl this round, however, but holds it in readiness, on its extended first leg, until the prey appears, when the droplet is hurled at it. If the aim is good, the sticky drop will capture the fly, which is pulled up by the spider.

It is rather interesting to note that three devices of man, the fishing-net, the net of the retiarius, and the bolas of the Gaucho had long been anticipated by spiders.

Hunting-Spiders

The spiders which do not spin webs catch their prey as a rule by far simpler means. They might be divided into :—

1. Simple wandering, picking up what is encountered.
2. Hunting, overtaking prey by speed.
3. Jumping from a distance.
4. Lurking in concealment and seizing the passers-by.

Many of the Mygalomorphae are content to wait in their burrows with the lid raised just enough to enable them to peep out. If an insect chances to alight within their range of vision, they spring upon it and are back in their burrows with the lid closed down almost as quickly as the eye can follow them.

Many spiders are simple nocturnal wanderers with no permanent home. They rest hidden during the day and roam about in the dusk, seizing anything they may happen to come across. A common British spider which illustrates this is *Scotophoeus blackwallii* and it makes its habits evident to us when, as often happens, it gets into the bath or a basin and cannot escape. And so we find it there next morning.

The Lycosidae or wolf-spiders form the chief family of huntsmen. These spiders catch their prey by speed. The wanderers, Drassidae and Clubionidae, have perhaps the simplest possible task, for they merely grasp what comes their way, and the wolf-spiders show the first adaptation in the development of fleetness of foot.

Something a little more subtle is shown by jumping-spiders and crab-spiders.

Jumping-spiders, Salticidae, mentioned already because of their keen eyesight, form an extremely numerous group, widely spread throughout the hotter parts of the world, with representatives in the temperate regions. The little zebra spider, *Salticus scenicus*, is the commonest British species, and one which must be a familiar sight to many as it hunts over wooden palings. A jumping-spider creeps about its chosen area, whose colour it usually matches somewhat closely, and every now and again stops, and by straightening

its forelegs, raises its head and gazes round its neighbourhood. It may be that it espies an insect recently alighted, whereupon it approaches with such caution that its movements are quite imperceptible until it gets within jumping distance. Then it suddenly leaps with practically unerring aim and fixes its chelicerae in its prey. To hunt in this way on perpendicular surfaces demands a very secure foothold, which the spider obtains by the pad of hairs or scopula already described. At the same time an accident or an inaccurate leap is to be guarded against, and the spider does this by laying behind it a silk thread, bound down at frequent intervals. Like the mountaineer's rope, this thread will protect it from anything more serious than a few moments' dangling at its end.

Crab-Spiders

A third method is adopted by crab-spiders, the family Thomisidae. Many members of this family lurk among the fallen leaves which collect under hedges and in similar situations. Their speciality, to which they owe their name, is their ability to run backwards and sideways upon their unsuspecting victims. This simple method may be taken as the starting point from which some other more ambitious members of the family have diverged.

Instead of stopping on the ground, some Thomisidae conceal themselves in flowers. In colour they match the petals among which they lie, and thus may be overlooked by bees or butterflies which visit the flower in their search for pollen or nectar. A very well-known British spider, *Misumena vatia*, is a good example of this. It is a particularly interesting species because it has the power, more fully described in the next chapter, of altering its colour to suit its surroundings.

It is in a genus of crab-spiders that is found the most striking adaptation for disguise. This is *Phrynarachne*, an inhabitant of the East. The first species described was *Phrynarachne decipiens*, found in Java by H. O. Forbes. There is a butterfly in Malaya which has the habit of coming

to rest upon leaves which carry the droppings of birds. Upon leaves *Phrynarachne* spins a small irregular patch of white silk, which exactly resembles the outline of the dropping, even to the rounded drop on the lowest side where the more liquid portions start to flow away. In the middle of this web the black and white spider takes its stand and its black markings complete the deception by resembling the particles of black solid which customarily float in this material. On the occasion of Forbes' discovery, he saw the butterfly feeding, as he thought, as usual, and started to investigate what seemed to be its curious taste. To his surprise the butterfly allowed itself to be picked up, and it was not until then that he realised that it was being eaten by the spider. The little patch of web deceived both butterfly and man.

His first description of the occurrence naturally aroused a considerable interest, which was enhanced by what followed. More than a year later, when Forbes was collecting in Ceylon, the sight of a bird's dropping made him wonder why he had never found here the spider which he had previously encountered in Java. Then he looked again, more closely, and saw that here was indeed the spider, deceiving man for the second time. This species is known as *P. rothschildi.*

The Spider's Bite

Many of these spiders have to face an important problem when they tackle animals which possess poisonous stings. In many cases, their solution is the very remarkable habit of biting their prey in the one spot where an instantaneous quietus will follow—namely, the cervical ganglion. Fabre's experiments with wolf-spiders and large bees with formidable stings showed that a bite in the nape of the neck killed the bee instantaneously, but that a bite elsewhere did not prove fatal for several hours. The spiders were apparently aware both of this fact and of the dangerous character of their enemies, or at least they acted as if they were. For if they came upon the bee in a favourable position, they bit

it unhesitatingly, whereas in other circumstances they tended rather to avoid risks and to protect themselves.

Fabre's conclusions have, however, lately been questioned by Rabaud (1921).

Other Kinds of Food

Insects have been the quarry in all the foregoing instances of spiders' wiles, but there are a few spiders which hunt other game. Perhaps the most interesting is the spider first discovered in Natal, and since found also in the Persian Gulf and elsewhere, *Thalassius spenceri*. This spider, a member of the family Pisauridae, has very long legs and lives close to the water. It takes up its position with its two posterior legs resting on a stone ashore, and with the other six spread out upon the surface of the water, covering a large area. The tarsi indent but do not pierce the surface film and in this position the spider waits. If a fish passes below it, it makes a sudden dive, its whole body going under water. Its long legs are wrapped round the fish, which is bitten and dragged ashore. The spider then eats the fish with unusual speed, leaving nothing except the backbone! It has also been seen to eat tadpoles of the toad *Bufo carens* and adults of the small frog, *Rhappia marmorata*.

Spiders are, therefore, not exclusively insect-eaters. The bird-eating Mygalomorphae described in Chapter XIV illustrate a wider choice of food, and McCook's great work on American spiders gives instances of the capture of fish, mice, and snakes. Some of these are clearly much larger and stronger than the victorious spiders and raise the important question of the spider's poisoning powers.

The Venom of Spiders

Spiders' attacks on larger animals have been studied both in natural circumstances and in the laboratory. To the former group belong most of the cases described by McCook and the many similar instances scattered throughout books

of travel. There is no ground for doubting any of these, but in only a few instances has it been possible to be sure that the victim was in active health before the spider bit it.

On the other hand, the experiments of Fabre are more than mere descriptions of finding a large corpse in a spider's web. Fabre was working with the wolf-spider, *Lycosa narbonnensis*, common in his neighbourhood, and he induced it to bite a young sparrow in the leg and a mole in the nose. The bird almost immediately lost the use of its leg; after two days it refused food and died. The mole, too, gradually ceased to feed and died before the third day.

From these results it is justifiable to conclude that the bite of large spiders might be not wholly negligible in its effect on man. The ordinary European species do not seem to be dangerous, but they may be irritating. But it has been already explained why irritating results do not always follow, and why many experiments with artificially induced bites have given conflicting results. Walckenaer was unable to distinguish between a spider's bite and a prick with a needle, and the same result was stated by Blackwall after several experiments, described in his *Researches in Zoology*. Pickard-Cambridge noticed the discrepant nature of consequences, for spiders' bites on the fingers of one of his sons produced a small white swelling with surrounding inflammation and considerable itching and smarting; while similar bites on his own fingers were followed by none of these symptoms. Bertkau has also stated that he distinctly felt irritant poison, and my sister has given similar evidence. In August, 1926, she was, at my request, catching the spider *Segestria florentina* in Brittany. One spider showed vigorous resistance, in the course of which "it gave my finger a fierce bite and made it quite sore." The soreness lasted for the rest of the day, and it is noteworthy that this particular spider was being harried about and was consciously on the defensive.

The effect of spiders' bites on man is a very old problem, which has only lately emerged from contradiction and

obscurity to definite certainty. The early confusion was partly traceable to the legends surrounding the Tarantula, a small wolf-spider found in south Europe. As is well known, the supposed consequences of the spider's bite were a general melancholy, which proved fatal at last, unless a cure could be found in time. The sole cure was music. Those bitten, the tarantati, summoned a musician who played before them a variety of airs, or tarantellas, until he hit upon one that inspired the patient to dance. The following description is at least two hundred years old. "At first she lolled stupidly on a chair, while the instruments were playing some dull music. They touched, at length, the chord supposed to vibrate to her heart; and up she sprung with a hideous yell, staggered about the room like a drunken person, holding a handkerchief in both hands, raising them alternately, and moving in very true time. As the music grew brisker, her motions quickened, and she skipped about with great vigour and variety of steps, every now and then shrieking very loud." Such activity was supposed to cure the disease, the theory being that the poison was worked out of the system in perspiration.

Several writers in the seventeenth century devoted themselves to a discussion of tarantism, some of them with the avowed intention of discovering whether it were a genuine malady or not. Their descriptions of the symptoms agree well with one another, and not a few have been forced to conclude that the stories "were, in the main, true." Denial began in the Philosophical Transactions as long ago as 1672, where a Neopolitan doctor records the observed results of the tarantula's bite. "In a few hours after, the poor man was sorely afflicted with violent symptoms; as syncopes, very great agitations, giddiness of the head, and vomiting; but that without any inclination at all to dance, and without a desire of having any musical instruments."

As a matter of fact, the descriptions of the cures of tarantism give a clue to its origin. Wherever the tarantati are to dance, a place is prepared for them, hung about with ribbons and bunches of grapes. "The patients are dressed

in white, with red, green or yellow ribbons, those being their favourite colours. On their shoulders they cast a white scarf, let their hair fall loose about their ears, and throw their heads as far back as possible. They are exact copies of the ancient priestesses of Bacchus." When the introduction of Christianity put a stop to the public exhibition of heathen rites, the Bacchantes continued their profitable profession, but were obliged to offer some irrelevant explanation. The local spider best supplied their need.

The Tarantula myth died hard, partly because the name became appropriated for any large spider encountered by travellers and collectors in distant countries, while at the same time stories of the dangerous spiders, well known and feared abroad, were continually circulated. There was the Malmignatte of Corsica, the Vancho of Madagascar, the Katipo of New Zealand, the Black Widow of America. The fact that all these spiders have special names of their own is proof of the general dread they inspire, and the Cambridge Natural History may be referred to for typical instances of the supposed results of spider bites. For many years these reports had to be accepted with caution, for it was difficult to get indisputable evidence that a spider's bite had really been the cause of the symptoms described.

Quite recently, however, the whole question has been put on a scientific basis. The spiders which have so long been dreaded all belong to the genus *Latrodectus*. This genus belongs to the family Theridiidae and most of its species are black in colour with red or yellow markings. When once this fact is realised, it is possible to make experiments with the guilty species, and, as a result, American doctors have settled the question. Spiders of the genus *Latrodectus* will eat almost anything, including tarantulas, scorpions, woodlice, and lizards. The poisonous Spanish fly, *Cantharides*, is also eaten, apparently without its peculiar effect. The bite of the spider is dangerous to horses and camels; in 1903 Schtscherbina recorded the death of a camel due to a *Latrodectus*-bite in the upper lip. On the other hand, sheep and pigs can eat the spider unharmed,

and the former may be used to clear a field of the spider as an alternative to the usual method of burning.

Reese found that extracts from the poison-glands of *Latrodectus mactans* would quickly kill a cat. Kellog made the poison into pills with sugar and determined the effect of swallowing them. He experienced pains, depressed heart-beat, and constipation. Dr. Bogen, however, has furnished the most convincing evidence, based on fifteen patients which have been in his care at the Los Angeles General Hospital. In nearly all these cases the spider's bite was witnessed by the patient; the symptoms were pain in the legs and abdomen, extreme abdominal rigidity, high blood pressure, and high temperature. The chief remedies were warmth and large doses of opiates.

The most remarkable feature of arachnidism, or spider-bite poisoning, is its limitation to the spiders of one widely distributed genus. The bites of other spiders, often larger and stronger animals, do not seem to produce anything more than the inconvenience described above. Local pain and swelling have been recorded as the only results of the bites of the spiders *Tegenaria parietina*, *Chiracanthium nutrix*, *Argyroneta aquatica*, *Trochosa singoriensis*, and *Dendryphantes noxiosus*.

Few instances have been recorded of a dangerous bite from a spider other than a *Latrodectus*. One of these is a rather rare Australian trap-door spider, *Euctimena tibialis*, which bit a child in Sydney in February, 1927: the child died shortly afterwards. Tragedies like this are fortunately uncommon.

Another spider, locally known to be poisonous, is the Argentine species, *Glyptocranium gasteracanthoides*, called familiarly the Podadora. This spider lives in vines where it sits with its legs drawn in and closely resembling a vine-bud. It is thus unnoticed by the workers among the vines, who may get bitten in the hand, or in the foot when the spider has dropped to the ground. The bite becomes inflamed and swollen and takes from six to ten days to heal. Fatal cases have been known when the victim was bitten in

the throat and the swelling caused suffocation, or from blood-poisoning.

Walbum (1915) and Levy (1916) have investigated the chemical nature and physiological action of spider poison in some detail.

The poison is a strongly alkaline fluid, containing proteids which coagulate at 65°–75° C. It is soluble in water, and insoluble in alcohol or ether. Walbum showed that the body of the common garden-spider, *Epeira diademata*, contains four poisons :

(i) the poison of the chelicerae,
(ii) epeiratoxin,
(iii) epeiralysin,
(iv) epeiratrypsin.

The chelicerae-poison is less poisonous to warm-blooded animals than to flies or other arthropods, such as crayfish. This is in accordance with the spider's usual habits. Epeiratoxin is confined to female spiders and is contained in the developing eggs. It cannot be found in the spider in the summer, but appears towards the end of August and reaches a maximum concentration in late September. Its poisonous constituent is an albuminoid, which has a fatal effect if injected subcutaneously into the bodies of mice or cats. Epeiralysin is contained in spider's blood and epeiratrypsin in their digestive fluids.

Kobert and Schtscherbina have shown that from spider's blood an antitoxin against their chelicerae-poison can be prepared. The latter in 1903 so immunised a camel that it suffered only temporary effects from the bites of six *Latrodectus*. The antitoxin has not, however, been perfected for use outside research laboratories.

Drink

We turn to the less familiar fact that spiders frequently drink. In disposing of its captures the spider sucks out only the fluid parts of its prey. There is very little mastica-

tion, as we understand it, merely a chewing of the food between the mandibles to squeeze out the liquid. It is, therefore, rather surprising that they should require much else to drink, and yet they certainly do.

An early and well-known occurrence affords an instance of this. The arrival of many small gossamer spiders aboard the *Beagle* when sixty miles from the American coast was recorded by Darwin and has often been quoted as proof of the distance which spiders are able to travel by this means; but Darwin also recorded a fact which was quite as interesting, though seldom referred to, that the little creatures were very thirsty and eagerly drank up drops of rain-water.

Spiders kept in observation cages in the laboratory have to be given water at intervals and may often be seen to drink it; in fact some, particularly wolf-spiders, are incapable of living without it, however well they may be fed. The rearing of young spiders is never an easy task and it becomes even more difficult if water is not freely given. Help may be obtained from the fact that water is not the only fluid they will drink. I have supplied them at various times with drops of bovril and drops of beer, to their evident satisfaction, and there is also a record of their being fed on milk.

A particularly interesting record of the spider's necessity for water was published as long ago as 1882, by Campbell. He had a captive house-spider, which one day he found in a state of collapse on the bottom of the cage, evidently in extremis. He poured some water into the cage and the spider at once crawled to it and drank it. The long drink completely revived her, and her abdomen, previously shrunken, rapidly distended.

This distension of the spider's abdomen, which is often particularly obvious after a large meal, leads us to consider an important adaptation which spiders and some other Arachnida exhibit. They are capable of taking a relatively large quantity of food, when they are fortunate enough to obtain it, and it is, of course, when under observation in cages that their capabilities in this respect may best be seen. A spider which has killed and eaten another almost as big

as itself and is in consequence bloated with food will none the less not refuse to catch and suck flies. If a small spider is able to overcome a much larger one, as is often the case, the small victor may be seen feeding almost continuously for the next twenty-four hours. It is only before a moult that a spider refuses food.

Fasting

If overfeeding is continued it is not without effect. I had a particularly favoured *Tegenaria*, which, in response to a very liberal diet, laid twelve cocoons instead of the usual two or three. But the power to take these large quantities of food has a biological value—it is not a mere curiosity. The spider does not and could not use all the nutriment at once; much is stored in the branching diverticula of the abdominal portion of the intestine. This explains the distension of the abdomen, which could not possibly be caused by expansion of the central canal itself. From these diverticula the stored food is absorbed as required, and so it comes about that the spider is able to survive extraordinarily prolonged fasts. It should be pointed out that this statement is not a mere assumption, but one capable of experimental demonstration. If two spiders are kept for a week or so, one being starved while the other is well fed, and if they are then both killed, fixed, sectioned and suitably stained, with stains that differentiate the contents of the abdomen, the presence of the stored food-products in one and their absence from the other is perfectly clear.

It can be seen, therefore, that the spider may be indifferent to Fabre's question, which most animals must seek to answer with an affirmative, "Shall I dine to-day, or not." This is the power which enables the young spider to survive the period which elapses before it can feed itself; it continues to live on yolk, of which it is able to carry an unusually large amount. Fabre was considerably disturbed by the great activity displayed by young wolf-spiders during that period in which they are carried on their mother's back.

For they are continually being knocked off and forced to climb up again, and during these days they do not, according to Fabre, feed at all. It was this that led him to elaborate the fanciful hypothesis that they must be able to convert the radiant energy of the sun's heat into mechanical work, and so literally to live on sunshine. It is a pretty idea, typical of a philosopher-poet, but it need not be considered seriously. The spider's economy is not that of the green leaf. It is very difficult to be sure that the spider never eats an insect even smaller than itself, and they have been seen to leave their mother's back in order to drink, climbing up again when their thirst was assuaged.

We must conclude this account of the spider's power of abstinence by quoting Blackwall's testimony as to the length to which it may be carried. A female *Steatoda bipunctata* was caught in August, 1829, and fed until October 15th, when it was mature. It was then corked up in a bottle and kept in a bookcase, and was no longer fed. This spider fasted for thirty months, and died at the end of April, 1831. During all that time it was able to spin a new web when the old one was removed, which makes its feat of much greater interest than the prolonged fasts of such creatures as molluscs. These may survive years, but they do so in a state of suspended animation, in which the vital processes are reduced to a minimum.

CHAPTER VII

THE SPIDER'S WEB

THE most characteristic feature of the spider's life is its use of silk. As one writer has expressed it, the spider has hit upon the device of turning its food into silk and using it as a net to catch more food. Of the origin of this silk-producing habit it is difficult to speak definitely. In dealing with coxal glands, it has already been indicated that the silk glands may have originated by modification of this part of the excretory system. Thus silk was originally a waste product, but now fulfils a useful function; yet how the change from waste matter to a valuable substance came about must remain a matter of speculation.

SPIDERS' SILK

As things are now, we find that the spider produces relatively large quantities of a proteid in the form of a viscous fluid which rapidly hardens on exposure to air. The chief physical properties of the threads thus formed are their great tensile strength, which is second only to that of fused quartz fibres, and their high coefficient of elasticity.

Observation of spiders' habits soon shows that the making of a web is only one of the many uses to which the spider puts this valuable material. Through life the spider is completely dependent on its silk. At least two different classifications of the spider's silken products have been suggested, the first by Wagner and a later one by Montgomery. Yet another, more extensive than either, is suggested here, taking account of the three dimensions.

I. *Linear Constructions.*
- (i) The drag line.
- (ii) The parachute.

II. *Ribbons and Plane Structures.*
- (iii) The attachment discs.
- (iv) The swathing band.
- (v) The sheets of Theridiidae.
- (vi) The hackled band of cribellate spiders.
- (vii) The sperm-web.

III. *Solid Structures.*
- (viii) The web or snare.
- (ix) The egg-cocoon.
- (x) The nest or retreat. This may be
  - (*a*) a mere tube ;
  - (*b*) a silk-covered excavation ;
  - (*c*) an inverted cup near the web.
- (xi) The moulting chamber.
- (xii) The mating chamber.
- (xiii) The hibernating chamber.

The present chapter is mainly concerned with No. (viii) of the above list, most of the others being described in more appropriate places.

It is worth pausing a moment to settle the very old question of the value of the spider's silk to man. As long ago as 1710 a M. Bon, of Languedoc, make some silk stockings from this material. The Paris Académie des Sciences thereupon invited Réaumur to investigate the possibility of further use of spiders' silk, and his experiments proved conclusively that its utilisation on a large scale was impracticable. The ordinary silk of which the web is made is of no use whatever ; it cannot be worked. Only the cocoon silk is strong enough to stand manipulation, yet a single thread of the silkworm is equivalent to four or five spider threads. The silk is so torn in the process of spinning that its lustre is much impaired, and the larger number of threads which must be used means a corresponding increase in the air-spaces between them, which further

reduces reflection. The spiders themselves must be separated one from another to overcome their cannibal propensities. This involves much greater labour in feeding and housing them, and when, finally, it is realised that 57,000 spiders would be required to produce but a pound of silk, the project of profitable utilisation is seen to be a manifest impossibility.

Of course, this does not mean that the silk can never be spun, for several well-known and often-quoted examples prove the contrary. But these are isolated efforts.

There is one purpose for which a thread of spider's silk is the best material that can be obtained. Nothing else is so satisfactory for the threads which are placed across the lenses of optical instruments such as range-finders, cathetometers, and microscopes, for marking the centre of the circular field of vision. Even the scratch of a diamond is broad by comparison. The silk is collected in the autumn from the common orb-spiders, *Epeira diademata* and *Zilla atrica*. If a spider is picked up and the silk thread which is normally hanging from its spinnerets is gently pulled, the spider will emit more silk, and if the pulling is continued quite steadily a very long thread may be drawn out. In practice the thread is wound upon cards from which the centres have been cut, and which have been painted with gold size to hold the thread in position. On cold days, a spider must often be taken indoors to induce it to spin actively. When a card is wound, it is stored until the silk is required; this may not be until two years later, but the silk retains its elasticity and is just as workable as when fresh.

Sometimes the thread has been provided by all four ampullaceal glands, and is split, by skilled workers, into its four components. When once in position the threads remain in use for many years, and the whole process is of interest, because it is the only instance of commercial value in the spider or its products.

The Origin of the Web

One cannot do more than speculate as to the origin of the web. The primitive spider was undoubtedly a huntsman and the first use of silk was probably to form the drag-line which nearly all wandering and hunting-spiders still pay out behind them as they move. The glands which to-day produce this drag-line are present in every spider, and serve the same or similar function, such as the formation of the foundation lines of the web. Moreover, it is not impossible dimly to perceive how the excretory matter which was the forerunner of silk, might perhaps have been used occasionally in somewhat the same sort of manner. Granting this, we start with what may be called the drag-line habit. If this coexisted with the habit of taking shelter in a crevice, it is clear that the home or shelter of the spider would be coated within with the silk of accumulated drag-lines. Many of these, laid down when the spider left or returned to its retreat, would run outwards in all directions from the mouth of the crevice ; and the next assumption it is necessary to make is that the spider discovered that, as it rested at home, movement of these lines would imply the tripping-up of some passer-by, who might well be caught and eaten.

The Evolution of Webs

What has been sketched is, in any case, the possible origin of a common type of spider's domicile. The most primitive spiders known, the Liphistiomorphae, which have persisted almost unchanged since the Carboniferous Age, make homes which, with one addition, resemble precisely the one we have pictured. They consist of a tunnel-like hole lined with silk, with the edge of the lining drawn out all round the mouth in a fringe and held in position by radiating threads. The distinguishing feature of the Liphistiid nest is a trap-door, which may well be assumed to have been a later addition. Excluding the trap-door for

a moment, there is here the primitive type of web, consisting of an expansion of the tube which lines the burrow. Wandering insects which trip over the guy ropes or trespass upon the fringe give notice of their arrival to the spider within, who rushes out and secures them if possible. Liphistiidae are spiders practically confined to Indo-Malay, but webs of just this type are made by all the primitive web-spinners, such as the Dysderidae, a primitive family, not well represented in this country, though common in Europe. Almost every stone wall in northern France harbours the fine large spider, *Segestria florentina*, which lives in a web exactly corresponding to the description given above. A tap with a spike of grass on the fringe at once brings out the spider to investigate, and shows us a new feature.

It is evident that the gaping bell-mouth of our primitive web is not well protected against marauders, and it may be supposed that it was a reaction to this fact that resulted in both Liphistiidae and the Mygalomorphae spinning trap-doors to close the aperture. The trap-doors are thus conspicuous characteristics of these two sub-orders of spiders. In the third sub-order, the Arachnomorphae, there are no trap-doors : the primitive web is used in its open form, as in *Segestria*. But the spider rests in the tube with its third pair of legs turned forwards, so that it may use all six limbs against intruders.

The nearest British approach to the *Segestria* type of web is the cribellated web of the Amaurobiidae. These are the bluish, rough-looking webs so common in the corners of windows, in cellars and sheds, seen often diverging from crevices in wooden palings or keyholes of gates. With the addition of the carded silk laid on by the calamistrum this web resembles our primitive type in all essentials. It differs from it only in having the fringe portion relatively much larger ; and the advantage of making the fringe cover a wide area is obvious. It not only gives greater opportunity for catching flies, but it affords greater protection. It becomes so difficult to

approach the open tube without becoming entangled, that the spider has less need for caution when it is at home, and the third pair of legs have resumed their more convenient, normal, direction.

The next stage leads to that type of web seen most familiarly in the ordinary cobweb, spun by the house-spiders, *Tegenaria*. Here a silk tube is still present as the resting-place of the spider and the expansion of the fringe has been almost confined to its lower edge, which is now spread out horizontally as a hammock-like sheet. In favourable situations, as, for instance, between the rafters of a shed roof, this hammock may reach great lengths. In its simplest form this type of web is spun by the genus *Coelotes*, belonging to the same family, the Agelenidae, as house-spiders, but living out of doors, in dark, damp situations under stones. It is seen again in the common *Agelena labyrinthica*, whose gleaming white web is a conspicuous ornament to gorse bushes in August; and it is a significant fact that the young of *Agelena* spin their webs close to the ground, only the adults occupying high situations in the bushes. These webs well illustrate the next addition, that of threads whose original function was to support the sheet, being stretched above and below it among the branches. Flying insects would strike against these supporting threads and be thrown down on to the sheet, and now there are many more threads above the sheet than would really be necessary for support. They make a valuable addition to the effective area of the web, and it may be supposed that they have been multiplied for that purpose.

This indicates a gradual change from the fringe, which caught the wandering creature, to the hammock and its superstructure more likely to catch those that fly. The web is assuming its true function.

The tendency to raise the web to places where flying insects are more likely to blunder into it can now be understood, but in such situations the tube will have no place. The Agelenidae retain it, but for most it is too conspicuous

and is accordingly abandoned, while the spider itself takes its position on the underside of the sheet. This common type of web is spun by the family Linyphiidae. Every bramble bush shows examples; the hammock-like sheet and the inverted position of the spider beneath it make webs of this family easy to recognise. Numerous spiders have adopted this type, a fact which is evidence of its success. Yet it is none the less open to objections. It has to be spun in conspicuous places, and the closely woven sheet offers dangerous resistance to the wind.

It seems that two different means have been adopted to avoid these disadvantages. A sub-family of the Linyphiidae has taken the web down again to situations near the ground. Here among grasses and over depressions in the soil they spin a sheet with generally but a minimum of superstructure, and the immense numbers of these small "money-spiders" is proof that both web and situation are satisfactory. The alternative is to abandon the sheet, but to keep the branching threads, with the addition of a small cup-like retreat to protect and conceal the owner. This is the web of the family Theridiidae, whose members are very common in hedges and holly trees in summer. The web consists merely of an apparently haphazard tangle of threads, of all lengths and in all directions. It is interesting to notice that such a maze might well be thought to be the simplest possible type of web, the starting-point from which the other designs might have been evolved, as chaos gave place to order. On this assumption McCook has, indeed, worked out a partial scheme of evolution of spiders' webs. But our present train of thought does not support this view; the tangle of the Theridiidae is seen to be degenerate rather than primitive, simplified rather than simple.

The last remaining type of web is the circular orb-web of the Epeiridae, as beautiful as it is familiar. It is at first sight impossible to derive this web from any of the others which have found their natural places in the series, and no doubt the step which produced the finished product of to-day was a long one. The difficulty is partly in our own

mind, for the symmetry of the web produces the subconscious idea that the manufacture of such a masterpiece must be a complex, and even a deliberately skilful process. It has, however, been shown in Chapter V that the working of the spider's mind is such as to discount at once any idea of conscious design or elaboration. It is useless to look for signs of a higher mentality, and search must be made elsewhere.

Can there be found any cause for dissatisfaction with the Linyphiid web? Surely there can, for in its attempt to render more or less impenetrable not an area but a space it is wasteful of silk. Human fishermen are content with a plane net of two dimensions, and there can be no advantage to the spider in trying to work in three. It is therefore necessary to make the apparently surprising assumption that the evolution of the orb-web was yet another process of simplification. This view is supported by the following considerations.

If one of the webs of the Linyphiidae be examined, it will be seen that many of the superstructural threads are independent perpendiculars. These were probably put into place by the usual method of dropping on a thread and anchoring it at the point of arrest. The Epeiridae use the same method for placing the outlines of their webs. Is not the clue to be found here? The web of the Linyphiidae was improved by the Theridiidae, who merely omitted the sheet; the Epeiridae have made the next step by rearranging the tangle that was left. To drop a pair of vertical threads and to pass across from one to the other is, by slight repetition, to produce a structure that cannot but suggest some of the radii of the orb-web. If these radii multiplied and were then cross-connected, a crude form of orb-web might result, without as yet, of course, any of the conspicuous symmetry which forms so characteristic a feature of the orb-web to-day. It may be suggested that the symmetrical result is produced by the simplest process which covers the given area uniformly. Simplicity of movement is the keynote of the spider's method, and is later described.

Man is deceived by the beauty and symmetry of the result into imagining that the web must have been made by intricate means, such as would, for him, involve much preparation and practice. The point to be emphasised is that simplicity of construction has selection-value, and that beauty is a secondary accompaniment. Many instances of this may be found elsewhere.

The Making of a Web

The primitive types of web are not so much made as allowed to grow. A spider like a *Segestria* or an *Amaurobius*, after choosing its crevice does not immediately set about lining it and spinning the surrounding fringe, but during the evening it may be seen to be making a beginning by surveying its immediate neighbourhood and trailing silk as it goes. Repetition of this process will soon produce the web as we see it, but it may be some days before it reaches an advanced state.

The house-spiders which spin the common cob-web have not altogether abandoned this rough-and-ready method, and since they live most contentedly in captivity, their operations may readily be watched. When a *Tegenaria* is first put into a new cage, she devotes some time to exploration, without showing any extreme desire to escape. When she has found the darkest corner, she settles down into it and seldom moves again until the evening. During the first night she produces a passable tube of silk in this corner, with two or three main threads diverging from it and attached to distant points on the side of the cage. The cross-threads between these main lines are few, and indeed, during the first day, the spider is lucky if she succeeds in catching anything with this skeleton of a web. Every evening thereafter the spider repeats the promenade about its domain. Its long anterior spinnerets diverge from each other as they actively secrete silk, and the abdomen is moved from side to side with a peculiar swaying motion. As a consequence, a criss-cross of threads is laid down all

over the sheet, and the whole of the web gets thicker and thicker as long as it is inhabited. The spider can often be seen adding silk to the sheet while she is trying to catch an insect. If the web is shaken once or twice by the insect, while it moves about without being as yet entangled, the spider usually comes out to investigate. In so doing she spreads out her spinnerets and starts to broadcast silk. This might be generously interpreted as actuated by the idea of so improving the web that the elusive fly will soon be caught; but it is better interpreted as a survival of the dragline habit of the hunting ancestor, evoked by the action of hunting for promised food.

By these occasional additions of silk the holes which appear in the web as the result both of accidents and of normal use are gradually mended. As previously indicated, the spider's mental powers do not enable it to enter upon any instinctive process in the middle, so to speak; and the operation of putting a patch over a tear would be quite beyond it. The patching or mending is, however, effected by this gradual desultory activity to which we have referred.

Spinning the Orb-web

Only in the webs spun by the higher families of spiders is the operation of spinning carried out in its entirety by a sustained effort. The process of spinning the orb-web is one which many have watched, at least in part, and one which has been several times described. It is one of the many sights which must be seen to be appreciated, and it is really impossible to do justice to it in words.

The finished orb-web consists of five essential parts—the framework of foundation lines, the radial threads, the viscid spiral, the notched zone, and the hub. In addition to this there is a temporary non-viscid spiral used as scaffolding during the spinning, and there is often a thread which joins the hub to the spider's retreat.

The making of the web begins with the laying of the foundation lines. Fixing a thread to its starting-point, the

spider pays out a horizontal thread to some distant spot, crawling there with the silk held clear of obstacles by one of its fourth legs stretched out behind. The spider then allows itself to drop from the two ends of this line on threads which are ultimately attached to whatever it may be that brings the spider to rest. Lastly, the quadrilateral is completed by taking a thread, fastened to the bottom of one of the perpendiculars, to the bottom of the other, by walking round the three sides.

In this description it is assumed that a favourable situation for laying the first thread has been found. The spider, however, is often in a position from which it is impossible to pay out this line by merely crawling. In these circumstances, the spider makes use of the wind. Turning its spinnerets upwards, it exudes a droplet of silk, which the least breeze carries out into a long floating thread. This thread secures the necessary additional buoyancy by having a tuft of silk at its far end. While it is being wafted about the spider holds it up on the claws of one of its second pair of legs, and thus is able to feel when the thread comes to anchor on some suitable object. The framework is now strengthened by the spider, who travels all round it two or three times, adding a thread on each journey.

The radii are now added. The first two are stretched from corner to corner, after which the spider places them alternately on opposite sides of the centre, and with a truly wonderful ability makes almost equal angles all round. When the last radius is fixed to the framework, the spider returns to the centre and spins a rough spiral of four or five turns of ordinary thread. This is, of course, spun from the hub outwards, towards the circumference. Its purpose is that of a temporary scaffolding, to provide foothold to the spider when fixing the viscid spiral.

When the laying down of this spiral commences, the spider changes the character of its movements, which, from being rapid and spasmodic, become slow and deliberate. It is all but imperturbable, circling on, heedless of noise,

heedless of winds, or anything save actual disturbance of itself. The viscous thread is applied to the radii from the outside, working inwards, forming a nearly perfect logarithmic spiral. As each attachment to a radius is made, the viscous thread is rapidly stretched by the outside leg of the fourth pair. This causes the sticky secretion which covers it in a uniform cylinder to break up and collect, under the action of surface tension, in a number of equally spaced drops. The spider can work either clockwise or counter-clockwise with equal speed and accuracy ; it avoids treading on the new viscid thread, and as this line approaches each turn of the scaffolding, the latter is rolled up.

Finally the viscid spiral comes to an end a little way from the centre. The spider returns to the hub, where she eats the small silk ball made from the rolled-up scaffolding, and sometimes converts the centre of the web into a circle by eating also the cushion formed by the crossing radii.

The notched zone is added last. It consists of a few turns of spiral in which the circular thread leaves each radius slightly below the point at which it arrives. This gives stability to the central area and provides the spider with something to stand on.

The entire process of web-spinning is completed in less than an hour ; and, since the web is often seriously damaged in the course of a night's chase, it is generally repeated each suitable evening during a great part of the spider's life. The same foundation lines are used as long as circumstances permit.

Geometry of the Orb-web

Fabre, who devotes a chapter to the geometry of the orb-web, makes little effort, beyond a few speculations, to decide how the symmetry is obtained. Hingston, however, has more recently examined with extreme care the methods by which the spider makes her " measurements " of angles and distances ; and he has, at each step, confirmed his

ideas by direct experiment. In this he has made a very real addition to our understanding of the spider's art.

It is worth noticing here that the spider's accuracy, although of a high order, is not perfect. The finished web satisfies the eye, but looked at critically, it shows several places where the arrangement is not absolutely precise. If corresponding parts of the web be measured, the asymmetry becomes more obvious. It is asking too much of the spider to expect mathematical exactness; Nature does not concern herself with unnecessary refinements, and the spider's web is accurate enough for its purpose.

The first problem is the symmetrical disposing of the radii. The spider, standing at the middle of its web, feels with its forelegs the radii which have been already laid down, as if determining their positions. When it finds too big a space, it starts to fill it up by carrying out another radius. It runs along the neighbouring radial thread, and when it reaches the circumference, determines the position of the new radius by taking a fixed number of steps along the foundation line. Thus it is putting down a series of radii separated by angles which are subtended by equal arcs along the circumference. If the foundation lines were in the form of a circle, the angles at the centre would be accurately equal. The foundation lines, however, form a quadrilateral or a triangle, so that the angles cannot be exactly equal, but the spider is employing a simple method of obtaining results which are satisfactory. On occasions, too, something causes it to modify its usual method to the extent of attaching the radius to the circumference with a Y-shaped bifurcation of the thread. This often occurs in the corners of the original quadrilateral.

The second problem of measurement is the position of the non-viscid spiral. The spider begins this from near the hub; one of its forelegs touches the centre where the radii cross, and with the length of its own body it measures off the distance at which the first spiral is to start. There it applies its spinnerets to a radius, and begins to pay out the spiral line, rotating about the centre. But this process

would make a circle, not a spiral; therefore as the spider turns round, the foreleg is gradually extended more and more until, when the first round is completed, the leg can be drawn in and placed on the spot at which the spiral began. Further circlings with the foreleg on the inner spiral turn, and the spinnerets still paying out the thread, will complete the four or five circles of non-viscid spiral, each a measured body-length from the turn within.

The third and last problem is the accurate placing of

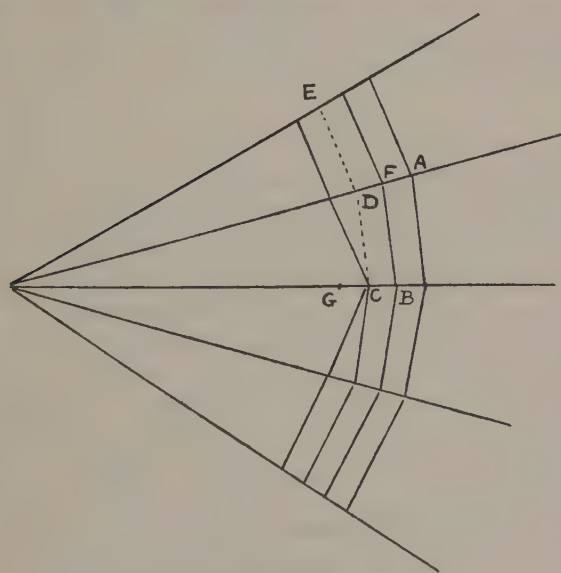


FIG. 65.—Making an Orb-web.

the viscid spiral. The spider puts down the outermost ring of this by taking the same number of outward steps from the last ring of the first spiral before it fixes the viscid thread in position. In this way the first ring is measured out all the way round, and all the inner turns of spiral are "reckoned" from it. At the moment of attaching the viscid thread with the fourth leg, the spider is feeling with its first leg the position of the point of attachment of the outer ring in the segment next in front. Thus, in Fig. 65,

the first tarsus is touching the point A when the fourth tarsus attaches the thread at the point B. This vital feature of the process of web-spinning is one of Hingston's best discoveries. It explains the apparently miraculous geometry of the spider, and it can be tested experimentally. Hingston himself did this, with the result shown in Fig. 65. The portion CDE of the spiral was removed, with the result that the spider, feeling on its next round for the point D, found instead the point F. It thus attached its thread at C instead of at G. The alternative method of testing this explanation is the removal of the tip of the foreleg. When this was done, the result is a badly made, untidy web.

The Webs of Young Spiders

By these devices, then, the orb-web is completed and the importance of the fact that it is constructed by an instinctive process, and not by imitation or learning, has already been mentioned. The webs which are spun by immature and very young spiders afford additional proof of this. Ten minutes' observation of the orb-webs on any blackberry bush in August will illustrate the point, for the webs will be found inhabited by spiders of all ages and sizes, and yet all will be perfect in form and symmetry. Montgomery has made a particularly careful study of this fact, as illustrated by the orb-weavers, *Epeira sclopetaria* and *Epeira marmorea*. After an exhaustive comparison of a number of webs of these two species, he was able to state that the first webs which the newly-hatched spiderling spins show all the essential parts of the webs made by the adults. The adults' webs are bigger when absolute dimensions are compared, but then the spiderling is a very much smaller animal and its web is relatively quite as efficient. It catches less, but less is required. The following figures, given by Montgomery, compare the first and last webs of *Epeira sclopetaria*.

	Average number of radii.	Average number of spirals.	Average diameter.
First web . .	15	16	7·6 cms.
Adult web . .	19	35	35·6 cms.

The webs spun by the male Epeirid spiders are indistinguishable from those of the females, until the penultimate moult, when the male webs are of smaller diameter. This might be expected, for at this age the males are smaller than their mates. The adult males of most spiders make no webs, only a nest close to the web of the female.

Divergences from Pattern

The orb-web described in the past few pages might be called the simple or primary type. A number of modifications of this pattern are made by members of the very large family of Epeiridae, and some of these are of interest.

The commonest type of minor divergence from the standard is found when the situation for the original framework is not altogether favourable. In such circumstances, the foundation lines often form a triangle instead of a quadrilateral, and the result is that the hub, where the radii cross, is much nearer to one side of the space than the other. If a web were made about such a hub in the ordinary way, a large proportion of the space would be empty of spiral and therefore wasted. The spider therefore spins an asymmetrical web which has more turns of spiral thread on one side than on the other. It does not add these extra turns all together at the end or at the beginning of the spinning of the spiral, but interposes them now and again by reversing its direction and passing over an arc twice or more. The question to be answered is—how does the spider know when to reverse and put an extra thread into a given arc? Hingston has observed that it turns on reaching a radial thread of sufficient length. If the hub is excentric, it must be supported by radii which are all of different lengths and therefore of different tensions, the tension in the short threads being greater than in the long threads. In other words, short radii are tight, long radii are slack. It is the spider's perception of a sufficiently slack radius which induces it to turn. There is perhaps no better example of the delicacy of the spider's sense of

touch than this ability to differentiate between the tensions of these threads, minute as such differences must be. There is, however, no doubt that tension is the determining factor, for when, in Hingston's experiments, he had cut certain threads and thereby caused some of the radii to slacken, the spider, as it spun blindly on, reversed at such points, even though reversal was unnecessary and destroyed symmetry instead of improving it.

The modification of the orb-web which is oftenest seen in England, is the sectoral web of the genus *Zilla* (Fig. 75). This resembles in every way the ordinary Epeirid web, save that the spiral thread is missing from two adjacent segments, leaving a bare radius. At the end of this radius is the retreat of the spider, who runs along it from its hiding-place to the centre of the web. The interrupted spiral of this web is not put in by a series of broken circlings, but by repeated reversals, the spider spinning clockwise and counter-clockwise alternately. It is interesting to note, in this connection, that the radii bounding the bare sector are longer than their immediate predecessors, and the peculiarity of the web may have originated from this fact. But the web is often spun so that the centre is asymmetrically placed, in which case these radii might not be as long as many others.

Protection for the Web-Spider

It must often have occurred to naturalists that the customary position of a spider in the middle of its web is one in which the creature is continuously exposed to every enemy with no protection whatever. One must assume that the risks are not sufficiently great to imperil the survival of the different species, and in temperate parts of the world this is probably true. In warmer countries, however, the case is different. Where the forms of life are numerous, competition is fiercer and living more strenuous. It becomes necessary for the web-spider to adopt some protective device.

Since a large proportion of the study of spiders has been by European zoologists, these methods of protection have been naturally neglected. Moreover, some of them were misunderstood and thought to be methods of strengthening the web, though there is no evidence that any spider ever requires a stronger web than it usually makes.

A recent paper by Hingston, however, describes a number of protective devices in orb-spiders' webs, all of

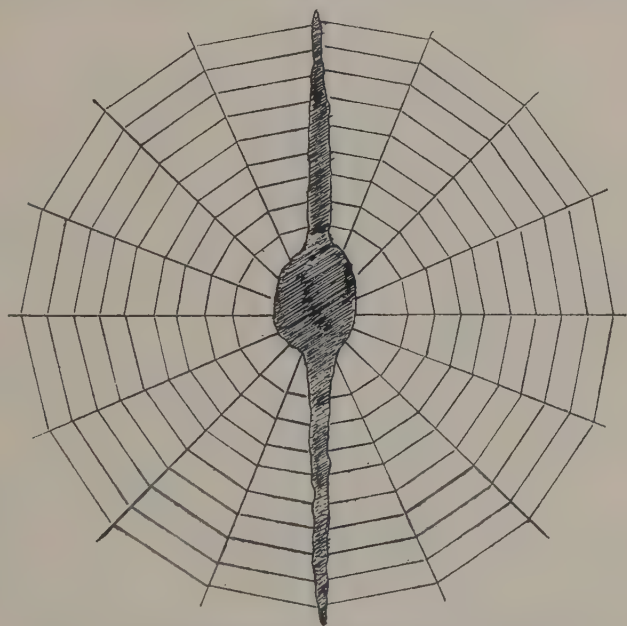


FIG. 66.—Web of Uloborus scutifaciens. After Hingston.

which take the form of an addition to the plain web. Some of these completely hide the spider, others make it so inconspicuous that it is as well protected as if it were invisible, others merely deceive the observer by methods of camouflage, by distracting attention or providing alternatives. Many present combinations of two of these methods.

Complete concealment is the most straightforward.

For example, a *Tetragnatha*, found in the Nikobar Islands, rolls up a leaf which it attaches to the middle of its large web. It rests inside the leafy cylinder, completely hidden. The majority of spiders which seek concealment in this way make their shield for themselves. The Uloboridae are a family of spiders which possess a calamistrum and a cribellum, and spin orb-webs like those of the Epeiridae. One of their species, *Uloborus scutifaciens*, adds a thick silk mat, interwoven with pieces of debris, to the centre of its web. Sometimes it is drawn out at one side so as to stretch from the centre to the edge of the web, sometimes it reaches right across from top to bottom (Fig. 66). The spider gets behind the central shield, between the web and the tree-trunk against which it is usually spun, and is quite hidden. A similar concealing shield is made by an orb-weaver found at a height of 15,000 feet on the Tibetan plateau, and is of interest because it shows that tropical conditions are not necessarily co-extensive with these protective schemes.

Another *Uloborid* spider adds either a well-defined white strap of silk lying obliquely across the centre of the web, or two such straps in the form of St. Andrew's cross. It similarly hides behind the strips of silk.

A *Cyclosa* from Burmah illustrates an extension of this mode of concealment. It spins the central shield, and round it adds a rough spiral of thick silk ribbon. This spiral has a protective value, for it tends to distract the eye from the centre, the vital point. We shall see that the other modes of protection which spiders adopt are all found acting either by themselves or in combination with a similar dispersal device.

Cyclosa is a widely distributed genus, and the single species which inhabits Great Britain illustrates the second type of protection—that of protection by blending. The British *Cyclosa conica* spins the usual orb-web, to which it adds an accumulation of silk, dry corpses, and other debris in the form of a band across the web. The band is interrupted in the middle, and in this space the spider sits.

Several spiders, including both Epeiridae and Uloboridae, from Asia and also from America, spin similar webs, all with the addition of a band of fluffy substance diametrically placed. In all cases there is a central gap into which the spider exactly fits. In the tropical examples, the spider's pattern makes it blend so perfectly with the bands that they seem to be a continuous strip. In *Cyclosa conica* the blending is far less perfect, so that the purpose of the

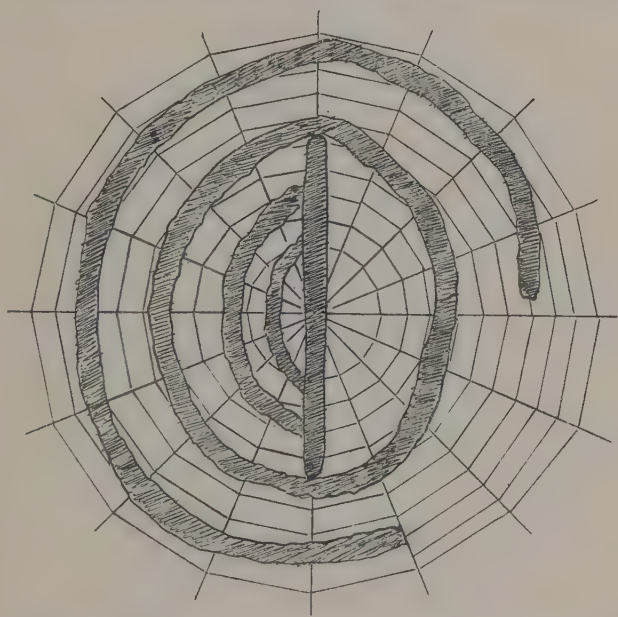


FIG. 67.—Web with dispersing bands. After Hingston.

fluffy strips was not understood, and they were thought to help in the entanglement of insects. A study of tropical forms makes it clear that the self-protecting habit has degenerated where competition is less severe.

These blending ribbons may combine with additional bands which encircle them, the result being to disperse and distract the sight. A spider from Burmah spins the two together as shown in Fig. 67. Another, a *Cyclosa*, spins a

central mat, and rests upon it, not behind it. It is inconspicuous because it blends with the mat, and a spiral of silk surrounding it assists in concealing it by distracting the eye.

A degree more subtle than either of the foregoing methods is the method of confusion, as illustrated in Fig. 68. In this method the spider is in sight, but owing

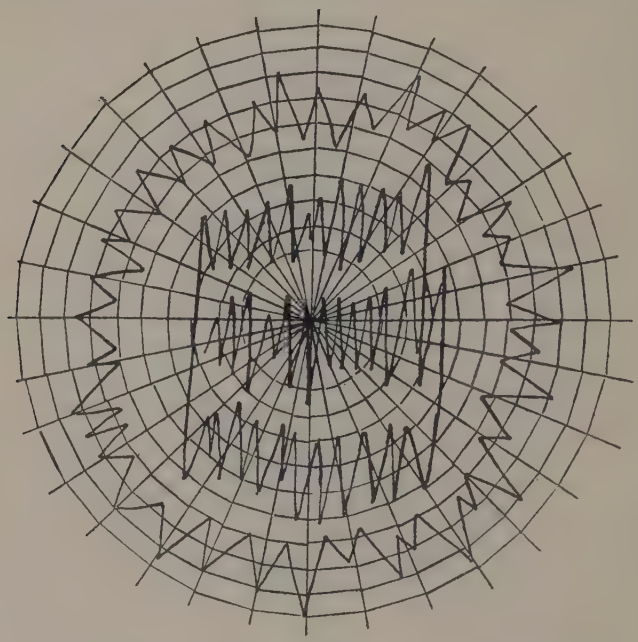


FIG. 68.—Web with dispersing zigzags. After Hingston.

to the confusion of threads around it, it is difficult to distinguish. The example shown has the addition of a zigzag thread round it which helps matters by dispersing sight, and others are known in which the central confusing threads alone are used.

Some of the most beautiful examples of protection show a combination of blending and confusion. The zigzag cross spun by *Argiope pulchella* and several other Indian

spiders is shown in Fig. 69. In four places, two adjacent radii are bound with a broad thread of silk, forming an X-shaped figure. The spider occupies the centre, its legs grouped in pairs along the arms of the cross, and its body coloration so assists in the deception that it no longer looks like a living object. One species, *Argiope catenulata*, spins three of these silvery zigzags. Its own cephalothorax is of the same silvery colour, and on its abdomen three bands of

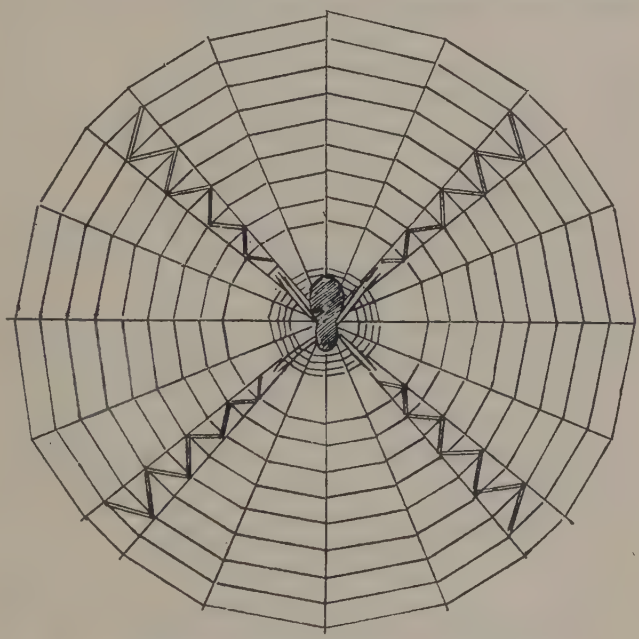


FIG. 69.—Web of Argiope pulchella. After Hingston.

this colour fall into continuity with the silk bands of the web. As a result, the spider, strikingly coloured when seen elsewhere, is almost invisible in the centre of its web.

A type of protection rather different from any of the foregoing is adopted by spiders who add to their webs objects which might be mistaken for themselves. Clearly, if a web holds four apparent spiders, three of which are dummies or decoys, the real spider has a more than sporting

chance of escape from any visiting raider. A Himalayan *Cyclosa* has the common habit of swathing its captures in silk, and these it hangs up one beneath the other in its web. It exactly resembles one of these parcels itself. So close is the imitation that it is impossible to distinguish the spider from its mummied flies by sight alone. Observers, even when encouraged by a bet, have failed to pick out the spider from the row.

Other spiders make their decoys in other ways. Thus *Cyclosa centrifaciens* makes two heaps of silk and insect-remains above and below the centre of its web. Each heap closely resembles the spider itself, as it sits in the web between them, and it improves the resemblance by spinning a loose tangle of silk round each heap, imitating the notched zone round itself

The addition of encircling dispersal bands round a row of imitative pellets is also known, being found in the web of a spider in Northern India.

One may conclude that web-spinning has been a thoroughly successful habit, and that, as such, it has evolved along various directions. In its last stages, however, it is open to the objection that it entails too great an exposure of the web-spinner itself, to meet which there have been evolved the remarkable protective devices which we have just described.

CHAPTER VIII

THE SPIDER AND ITS ENVIRONMENT

THE problem which continually faces every spider, as well as every other adult creature, is that of survival. During extreme youth, the solution of this problem is sometimes undertaken by the mother, but maternal care is not conspicuous among spiders. During immaturity, the survival of the individual is all that needs to be taken into account, until later in life there is added the more serious question of the survival of the race. This comes to mean that the actions of a spider will in general be directed towards one of four ends: protecting itself, feeding itself, reproducing itself, and, less frequently, caring for its young. Let us consider the first of the aims—that of self-protection.

Apart from the physical conditions of heat and cold, flood and drought over which the spider has no control, and of which it seems to take little notice, the spider is at all times exposed to the attacks of enemies. We shall conclude this chapter by a special consideration of these opponents, which include larger animals, to whom the spider is less than a mouthful, smaller one whose envenomed sting may pierce nerve-centres and paralyse limbs, and still smaller ones that insidiously lay their eggs as parasites upon the spider host. All these enemies have to be avoided, if possible, and it is this that the spider largely spends its time in doing. "Life," as Brindley used to say at Cambridge, "is one long struggle to get out of the way."

The spider's solution of the difficulty is in the main a passive one—that of not being seen, or, if seen, of looking like something that is not a spider. To achieve this it has peculiarities of colour and shape.

The Colours of Spiders

According to their general colouring spiders may be roughly arranged in four groups.

The arboreal spiders, which live among flowers and among the alternating light and shadow of the leaves, have usually a variegated colour pattern. Their relatives, who live lower in the bushes, are darker. The Linyphiidae, for example, which hang beneath their hammock webs have the lower surface of the abdomen dark, and the upper side marked transversely with bars of black and white. This is an interesting arrangement, because it reverses the usual colouring of animals. As is well known, many creatures, such as birds and fish, are dark above and light below, thereby acquiring a degree of invisibility against either the ground beneath them or the sky above. The Linyphiid spiders retain this by themselves living upside down.

The webs spun close to the ground, in hoof marks and similar small depressions, are inhabited by a numerous race of tiny "money-spiders," practically all of which have black abdomens with no pattern at all. Then, again, the house-spiders and others that live in tubular webs show a colour-scheme that may best be described as dusky, while the spiders that wander in search of their prey are of a greyish colour which blends well with the ground over which they hunt. All these varied colour schemes render the spider inconspicuous in their normal activities, but there are some instances in which colour plays a more active part.

There is, for example, a common British wolf-spider, *Trochosa picta*, which lives in sandy places and shows a pattern extremely inconspicuous against its sandy background. What makes it more interesting is the variation in the intensity of its colour to match the particular shade of sand prevalent in its neighbourhood. It is therefore of interest to inquire whether a colour which is apparently so vital to the spider that it changes in this way is, in actual fact, a protection. This has been tested by Bristowe, in a

haunt of the species where it lives in company with two others, *Trochosa terricola* and *Tarentula barbipes*. These two spiders are not protectively coloured to any great extent; and all three are exposed to the attack of wasps, which store them in cells as food for their grubs. Bristowe opened some of these cells and classified 35 spiders that he found inside. Two were *Trochosa picta* and all but one of the rest were *Trochosa terricola*, a fact that proves in a striking way the value of the coloration.

Colour is also of vital importance to the crab-spiders which lie in wait among the petals of flowers. None is more notable in this respect than the species called *Misumena vatia*, quite common in many parts of Britain and also found in America. This spider does not confine itself to flowers of one colour, but has the power of altering its colour to suit its surroundings. Almost white specimens are found in white flowers, yellow specimens in yellow flowers, and pale green specimens are sometimes to be found on holly leaves. The ability of this spider to change its colour has been the subject of several investigations, of which the most recent are those of Gabritschevsky. He bred the spiders from the cocoon, feeding them daily on the fruit-fly *Drosophila* or larger insects. They were kept in glass flasks and exposed to backgrounds of either white or yellow paper. The results of these experiments showed that only when mature were the spiders sensitive to the colours of their backgrounds. The white spiders when transferred to yellow paper assumed a yellow colour in a time which varied from as little as 24 hours to as much as 20 days. When these yellow spiders were replaced on white paper, they resumed their white appearance in five or six days. Their whiteness was due to the transparency of the hypodermis, which exposed guanin crystals present in the cells beneath; the yellow colour was caused by a yellow fluid which accumulated in some of the superficial cells.

There is still another way in which coloration may assist concealment, and that is by the exhibition of the so-

called flash-colours. These are best shown by certain tropical tree-frogs, whose general green colour is broken by patches of vivid red or yellow in the angles of the arms and legs. The result is that as the frog leaps from branch to branch, these colours appear momentarily as bright flashes. As the frog alights and resumes its resting position, the colours are suddenly eclipsed. The enemy in pursuit, following the conspicuous flashes, is actually looking a little ahead of the escaping frog. When the bright colours unexpectedly vanish, the eye must be brought back in search for the object, which has now faded into invisibility against the green leaves. Such a method of escape does not sound very convincing when thus described in print, but in reality it is remarkably efficient. It is a most astonishing experience when human eyes are looking for the spiders which illustrate the phenomenon.

The best known of these are *Tibellus oblongus* and its ally *Tibellus maritimus*, members of the family of crab-spiders. In form these spiders are very different from the majority of their family, for they are long and narrow; their colour is pale yellow marked with longitudinal brown streaks. They haunt sandy grass-grown spots such as sand-dunes, and when they run among the grass stems they are conspicuous enough. Then, suddenly, they stop, crouching along a blade of grass, their legs stretched out before and behind. In this position their brown marks, previously so clear, enable them to melt into their background and become extremely hard to see.

A really better example of the method is seen in the common British six-eyed spider, *Segestria senoculata*, which lives under the bark of fallen trees and in similar situations. Its abdomen has dark lozenge-shaped marks on its upper surface, and the femora of the legs have a bright tawny colour. As the spider runs the bright femora flash to and fro and catch the eye. When it suddenly stops, it folds its legs over its cephalothorax with the femora underneath, and the other joints stretched out above them. The bright colour of the femora thus suddenly

disappears, the spider apparently vanishes into thin air, and the closest scrutiny often fails to reveal it for several minutes. Perhaps the most remarkable feature of this method of protection is that it is not at all noticeable when one examines dead spiders in the laboratory. It is only when one has come up against it in collecting that one realises that it exists and how efficient it is.

The last way in which colours may be of value to a spider, apart from the colour patterns which are involved in mimicry, is as a warning. That is to say, they may be colours which other creatures have, by past experience, learnt to associate with a formidable antagonist. Such warning colours are oftenest yellow and black bands, shown most familiarly by the common wasps. There are certain trap-door spiders belonging to the genus *Poecilotheria* whose upper surface is dark coloured in the usual way, but whose sternum and underside are black, slashed with bands of yellow and white. When the spider is frightened it rears on its hind-legs, thus exposing its warning colours to any creature that may be threatening it.

The Shapes of Spiders

It has already been mentioned, in Chapter II, that many of the shapes of spiders seem to be without much purpose, although this is probably only another way of expressing our ignorance of the details of their mode of life. On the other hand, many of the shapes of spiders' bodies are of obvious protective value. They give the spider so close a resemblance to stationary objects in its neighbourhood that it must be very difficult for other animals to discover it.

Two instances of protective resemblance have been mentioned in the last two chapters—the spider *Phrynarachne*, which looks like a bird's dropping, and the *Cyclosa*, which hangs in its web a row of pellets each exactly like itself.

The African spider, *Cladomelea akermani*, is another very good example. It attaches its egg-cocoons to the

grass, binding several blades together to form a strong enough support. Here the row of five or six cocoons is a somewhat conspicuous object, but one which might easily be taken for the fruit of a shrub. The spider takes up a position beside the cocoons, and in her usual huddled-up state is almost indistinguishable from them. Close scrutiny is needed to determine which is the spider, and which her eggs.

Another African spider, *Menneus camelus*, is equally well protected. Akerman, who first described the way in which it uses its web, for some time believed that during the day the spider dropped from the bushes to a retreat near the ground. It was only by searching diligently along each twig that the spider was finally found. It sits close against the twig, which it grasps with its two pairs of hind legs, its fore-legs stretched out in front. In this position it looks like a part of the twig. Its abdomen bears a conical hump, to which it owes its name, and this, resembling a thorn or broken twig, adds largely to the deception.

Protective resemblances as close as these, which often defy men who are searching as carefully as they can and with a knowledge of what to expect and what to look for, cannot but be of value to the spider by enabling it to avoid detection.

Here it may well be pointed out that the concealment afforded by protective coloration and resemblance is enhanced by, if indeed it is not mainly dependent on, a disability of the vertebrate eye. For to the eye of the observer there is a clear distinction between seeing and perceiving.

The most familiar instance, which will explain this distinction, is the puzzle-drawing of one's childhood, which contained a " hidden " face. At first, even on close inspection, the face was quite invisible; but when at last it was recognised it became for ever after so conspicuous a feature of the picture that it seemed impossible that it could ever have been hidden.

The same must surely be true of the spider (or any

other animal) at rest, full in sight but protected by one of these methods. It is the collector's experience that such a spider is exceedingly difficult to detect; but when it has betrayed itself its outline, its light and shade take on an altogether new significance and the spider is easily perceived. Its hope of safety depended on its keeping still so as not to attract attention.

The whole thing emphasises the distinction between mind and brain, and may perhaps be due to the imperfection of the human eye. We are accustomed to regard the eye as wonderful, as it is, but that it is not faultless is also true. It has indeed been said that "it is so inexact and imperfect that one might almost suppose nature was trying to keep us from knowing what the world really looks like."

Mimicry in Spiders

In many other instances, the colours and shape of the spider give it a degree of resemblance to some other animal, on which the spider's enemies are not accustomed to prey. This is the phenomenon of mimicry, which is of wide occurrence through the animal kingdom. It is most strikingly shown by butterflies, which include many examples of models and mimics. The models are conspicuously coloured insects belonging to the pharmacophagous or poison-eating group. Because of their habit of feeding on plants with an unpleasant taste, they acquire an unpalatable flavour, and are therefore avoided by birds which have learned to associate their patterns with their nasty taste. Thus any other butterfly which can resemble this pattern will have a chance of sharing their immunity. Mimicry is an extremely specialised form of adaptation to environment, and in its explanation in the usual terms of natural selection there are many grave difficulties. With this, however, we are not at present concerned. The mimicry shown by spiders is slightly different in kind from that common among butterflies, since spiders do not mimic one another.

Instead they mimic other animals—among which are caterpillars, snails, beetles, and ants.

The spider *Ariamnes simulans* (Fig. 70) was discovered in Calcutta in 1880. It has a very remarkable abdomen, whose posterior end is produced into a long tapering " tail." Thus the spinnerets seem to occupy a position in the foremost quarter of the abdomen. The tail and abdomen are of a prevailing green colour, with silvery and yellow-brown marks, and the resemblance of the whole spider to a caterpillar is very close.

Several spiders are known which mimic snails, in Ceylon, Borneo, and North America. These spiders cling to the undersides of leaves with their legs drawn in, and in this position they are very like small snails, common in

FIG. 70.—Ariamnes simulans.

summer in similar situations. The spider remains immovable if the leaf is plucked, behaving as a snail would do in similar circumstances.

The beetles chiefly mimicked by spiders are the ladybirds, Coccinellidae, which are known to possess an unpleasant taste, and which flaunt vivid colours. These are closely imitated by several species of spiders belonging to the genus *Paraplectana* (Fig. 71) found in the East Indies, in Brazil, and in other tropical parts. Thus *Paraplectana thorntoni* is coral red with black spots, and exactly resembles a beetle, *Chilomenes lunata*, common in Natal. In Borneo the same or a closely related spider mimics the beetle *Caria dilatata*.

In addition, there are jumping-spiders of several genera which mimic little beetles of a squat oval shape. It is

probable, according to Pocock, that this resemblance is one of general shape and appearance, rather than precise mimicry of some particular species. All the beetle-mimicking spiders have short legs and a smooth regular abdomen which overlaps the cephalothorax to the extent of hiding the pedicle.

A Madagascan spider has been described with a curious flattened abdomen so shaped and coloured that the spider somewhat resembles a small butterfly. The likeness, however, is not very close, and it is doubtful whether this ought to be regarded as a true case of mimicry, especially since nothing is at present known of the spider's habits and habitat.

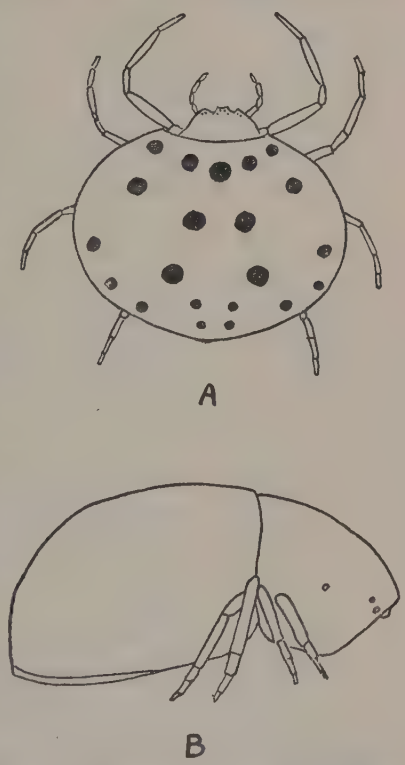


FIG. 71.—Beetle-mimicry by spiders. A, Paraplectana walleri. After Simon. B, Lysommanes tenuipes. After Pickard-Cambridge.

Most frequent and most precise is the mimicry of ants, and in Pocock's well-known paper on this subject no fewer than thirty-one different instances are mentioned. The general structure of ants is very different from that of a typical spider, so that considerable modifications in the spider's normal form have been needed to produce any degree of resemblance. Yet this has been done so thoroughly that in many instances the mimicry is remarkably perfect.

The cephalothorax is constricted in the middle to

imitate the ant's head and thorax, while the sides of the constriction are often masked by white hairs. The ends of the cephalothorax and abdomen are pointed, so that they grade into the pedicle and represent the ant's waist. In a few cases, even segments of the abdomen may be suggested by transverse bands of hairs. The legs of ant-like spiders are slender, and the first pair are frequently held out in front in imitation of antennae. Yet the resemblance does not end here. The characteristic activity and bustle with which the ant runs about is copied by the spider: it seems that it is not enough to look like an ant, there must be a mimicry of an ant's activity as well.

Fig. 72. — Myrmecium rufum. An ant-like spider. From Simon.

Only a few British spiders, such as *Micaria scintillans*, *Micryphantes beatus*, and *Linyphia furtiva*, show any resemblance to the ants among which they live, but ant-mimicry is much more common abroad. Ant-like spiders have been described from North, Tropical, and South America, from India, Ceylon, Malaya, and Japan. They include members of most of the families of wandering spiders, of the crab-spiders, and even of the web-spinning families, Epeiridae, Linyphiidae, and Theridiidae. The wolf-spiders seem to be without ant-like species, but there are many among the Salticidae or jumping-spiders. It is to this family that the mimicry is apparently most valuable. It is found in a few species of many of its genera, and one genus, *Myrmarachne*, of nearly a hundred species, is entirely given up to the mimicry of ants. The same thing is true of the family Clubionidae, one of whose genera, *Myrmecium*, consists entirely of ant-mimicking species. One species, *Myrmecium nigrum*, is shown in Fig. 72. It mimics the ant *Pachycondyla villosa*. Other

species of the same genus are yellow or red in colour, with brown or black abdominal stripes, resembling the ant genus *Megalomyrex*.

As among butterflies, the two sexes do not necessarily share the mimetic adaptation. A South African spider belonging to the family Eresidae, *Seothyra schreineri*, illustrates this. The females and immature males, which live in burrows in sandy parts of the veldt, are light brown and grey in colour, harmonising well with their surroundings. The mature males, which have to roam about, are quite different in colour, and mimic a vicious ant, *Camponotus fulvopilosus*, common in the locality.

It is noteworthy that the ants used as models are frequently those of formidable character. For example, *Myrmarachne providens* is an Oriental jumping spider which mimics the ant *Simo rufo-nigra*. This ant is a pugnacious creature, apparently quite fearless. It will attack almost anything it meets and its bite produces painful effects in human beings. Mutillidae are ants of similar aggressive habits, possessed of powerful jaws and frequently mimicked by spiders in many parts of the world. In Ceylon the spider *Coenoptychus pulchellus* is a well-known mimic of these ants. The spider has a reddish cephalothorax and a black abdomen, which in the male is marked with six large white spots, and in the female with four yellow spots. The male spider mimics the wingless ant, *Spilomutilla eltola*, and the female mimics the wingless female of the ant *Mutilla subintrans*. So close is the resemblance that at least two naturalists have recorded the fact that they have been deceived into picking up the harmless spiders with the precautions they would properly observe for ants! Mutillids are also the models for the Epeirid spider, *Ildibaha mutilloides* of tropical America: in this species the male alone is ant-like, the female is protected by a spiny abdomen.

One of the most curious instances of ant-mimicry is that of an Oriental crab-spider, *Amycioca forticeps*, which mimics the tailor-ant *Oecophylla smaragdina*. The spider is orange-red in colour, its cephalothorax is high and rounded

in front but narrowed and prolonged behind. Its abdomen is narrow and cylindrical, with a median constriction and narrowed at both ends. The hind portion bears two black spots. Thus the cephalothorax of the spider resembles the abdomen of the ant, while the abdomen of the spider resembles the ant's thorax, head, and eyes. When the spider escapes by running backwards, as is its usual habit, it mimics the ant running forwards.

This particular case illustrates another feature to which parallels are known among butterflies. The term "mimicry ring" is applied when the same model is mimicked by several different species, not necessarily members of the same family. The tailor-ant in question, *Oecophylla smaragdina* is mimicked in Singapore by another crab-spider, *Amycioea lineatipes*, in Ceylon by the jumping spider *Myrmarachne plataleoides*, as well as by other spiders and by the larvae of a moth. The Ceylonese mimic, *Myrmarachne plataleoides*, runs forwards in the usual way: the chelicerae, which are stretched out in front, are swollen at the ends and bear the black dots which represent the eyes of the ant.

There is, therefore, no doubt that mimicry is both real and useful, and constitutes an adaptation which confers great benefits on those that show it. This is proved by the fact that ant-like spiders often lay small numbers of eggs. The mimicry of ants by spiders is mimicry of the Batesian type, that is to say, it is mimicry of a dangerous animal by a harmless one, and benefits only the latter. Among butterflies a second type of mimicry, known as Müllerian, has been described. In this type two formidable species resemble each other, with the result that their natural enemies are educated to associate their appearance with their dangerous character twice as quickly as if their appearances were different. Those which are sacrificed in this education will be shared by the two species, each of which will lose only half the number they would otherwise have to give up. Mimicry of this type has not yet been detected among spiders.

It is of particular interest to note in conclusion that in this single order of spiders there are found good examples of protective coloration, protective resemblance and mimicry, adaptations which are usually illustrated by examples from widely different types.

Protective Habits

It must not be forgotten that these examples of coloration and mimicry include the exceptional spiders, rather than the great majority—at the outside a few hundred of the sixteen thousand known species. The rank and file are not protected in these ways, and it is only when we study their habits that we realise that they have evolved methods of self-protection which may counteract even the disadvantage of conspicuous colouring. Probably the most familiar example of a protective habit, which must tend to confuse and startle the onlooker and thus protect the spider, is the way in which garden-spiders shake their webs. The habit is common to several members of the family Epeiridae and is shared with the Pholcidae, of which the curious *Pholcus phalangioides* is the only representative in Great Britain. By vigorous contractions of the legs, the spider causes the whole web to oscillate with great rapidity, while it becomes itself no more than a blur.

Preening

We are justified in considering as one of these protective methods any action or habit which tends towards individual efficiency and proper functioning of the sense organs. Indeed, we often perform similar actions ourselves. The habit of preening, which makes for efficiency, is common among spiders, which are scrupulous in their attention to personal cleanliness and quite belie the popular notion that they are dirty. The habit was first described by Dufour, and is most frequently seen after the spider has finished a meal. It brushes the spiny tarsal joint of its palpi over the

front surface of its chelicerae, continuing to do so for some moments. It carefully brushes out the angle between the two joints of the chelicerae, as well as the narrow space between their two bases, and while it is doing this it is opening and shutting both parts of the chelicerae and moving them backwards and forwards.

I believe that the extending of this process to clean up all parts of the body was first described by myself in 1916. After examining the way in which large house-spiders are able to struggle along the surface of water, I noticed that, on their return to their cages, they one and all began to clean and dry themselves. This was a far more elaborate process than the mere rubbing of the chelicerae, and included the following operations :

1. The second and third pairs of legs were pulled slowly through the space above the lip between the maxillae. When the tip of the tarsus reached the maxillae it was held there motionless for some seconds.

2. The palpi were treated in the same way.

3. The first and fourth pair of legs were treated a little as in 1, but they were also carefully rubbed with the second and third legs, which were then immediately drawn through the maxillae again.

4. The sternum was rubbed by one of the metatarsi.

The separate actions did not take place in an orderly manner. A little of one was followed by a little of another, and often 2 and 3 were simultaneous. The spider worked from limb to limb and from side to side with no particular sequence. The whole operation took as long as half an hour.

It is probable that these actions are more than a mere scraping of the spider's surface. It will be recalled that the maxillae contain a system of rather mysterious glands, and the spider's actions lend support to the idea that the secretion of these glands is used as an ointment for the external surface of the body. There seems to be very little doubt of this in the particular instance recently described by Locket, and considered in Chapter XI.

The importance of this habit of cleaning the body is emphasised by the existence of a metatarsal comb specialised for this work, and found on the legs of certain spiders of the family Drassidae. On the undersides of the metatarsi of the four posterior legs, close to the tarsi and slightly to the outside, are two regular transverse rows of ten to twenty stout hairs (Fig. 73). These may be present in both sexes and at all ages. Berland has given an attractive description of his discovery of the use of the comb. He had caught near Paris a *Zelotes subterraneus*, and was about to kill it, thinking it could teach him no more, when it suddenly showed him the use of this "veritable peigne au sens propre du mot." It brushed different parts of its body, apparently to burnish the hairs and remove dirt. The third and fourth legs were used alternately, and the effects of the combing were so obvious that one could detect just where the comb had been applied. This comb is not found in every species in any one genus, and it does not seem to be confined to the Drassidae. What seems to be exactly the same thing is mentioned and figured in a paper by Pocock on Mygalomorph spiders of the Ethiopian region, published in 1897. It there occurs on the spider *Stasimopus oculatus* and is specified as part of the distinction between that species and *Stasimopus rufidens*.

FIG. 73.—Metatarsal Preening Comb.

CATALEPSY

The most generally distributed of these protective habits and one which is shown by spiders of practically every family is that already mentioned as the cataleptic reflex. This is usually described as "shamming dead," for several reasons an unfortunate term. In the first place, the positions assumed are not those of death, and it would be of little use if they were. As mentioned at the end of

this chapter, dead spiders are seldom found in Nature, and when, in collecting, one does chance upon a spider's corpse, it is very easily recognised. On the other hand, numberless small pieces of vegetable debris have to be looked at twice or more before one can be certain that they are not spiders in the cataleptic state.

Hunting and wandering spiders are generally induced to assume the cataleptic pose by a sudden tap in their neighbourhood, which causes them to draw in their legs, generally folded over their cephalothorax. Web-spinning spiders share the habit, and spontaneously drop from their webs on a thread of silk, an action which is familiar to most of us, since the commonest garden-spiders show it very readily. The spider seldom drops to the ground, if it can avoid doing so. If it passes a leaf on its fall, it usually checks its descent and creeps beneath the shelter until danger no longer threatens. It then climbs back to its web. Some spiders will drop from their webs far more easily than others. The commonest Linyphiid, *Linyphia triangularis*, whose web is to be found on every bush, is a particularly sensitive subject in this respect. The hand of the blackberry gatherer may but jar a twig more than a foot from its web, but down drops the spider into the prickly sanctuary beneath. A rarer English spider, *Theridion lunatum*, is, however, even more nervous. Its irregular webs are easily seen on the branches of trees in the few localities where it is plentiful, and to catch the spider it is only necessary to hold the net below and to touch the web ever so slightly. Down comes the spider without a second's delay.

W. H. Hudson described one of the prettiest instances of this habit, as shown by two South American spiders. These two spiders are found together ; one of them is the colour of the fresh green leaf, the other yellowish-brown, like a leaf that has faded and withered. The green spider falls somewhat quickly, as a green leaf would fall ; the brown one falls more slowly, as if it were lighter, like a dried leaf !

Autotomy

Another and a very familiar protective device, which spiders share with many of the lower animals, is that of casting off a leg. This is usually first encountered in collecting, for if one grasps, with fingers or forceps, the leg of an escaping spider, it is not long before that leg alone is all that remains in one's possession. This autotomy is closely associated with the spider's power of regeneration, or the reproduction of lost parts at the time of ecdysis. Autotomy is therefore more readily shown by immature spiders, which do not suffer a permanent loss, than by full-grown ones, which will not moult again. Regeneration is dealt with in Chapter XII.

It is important to understand that autotomy is quite distinct from forcibly wrenching off a limb. It is a reflex action, under the control of the nervous system. This may be proved by anaesthetising a spider with chloroform or ether. It may then be picked up by one leg, swung about and subjected generally to treatment which, in normal circumstances, would certainly provoke it to cast the leg. Again, if the spider is held in the fingers by one leg, it is possible to understand the action better. The other seven legs strain against one's hand, and the liberation follows a quite obvious jerk. If one holds the spider by two legs it seems to be unable to free itself in this way.

There must be some peculiarity of the blood system associated with the autotomy, or the spider would bleed to death. In the case of lobsters it is well known that the breaking point is constant, between the second and third joints of the limb, and that a special preformed membrane staunches the flow of blood. There must be something similar in spiders. The leg is cast from the trochanter, and no serious loss of blood follows. Indeed it is remarkable how little inconvenience the spider seems to suffer. But artificial amputation with scissors at other points in the leg is evidently a very different matter. Bleeding is profuse, until the spider puts the cut stump in its mouth.

In at least one instance, where the leg was cut through the middle of the femur and the remnant would not reach the mouth, I have known death to follow soon after the amputation.

Myrmecophilous Spiders

Many spiders have been driven by force of circumstance to adopt a life in close association with ants. In this they are not peculiar, for ants' nests might well be described as the caravanserai of the Arthropod world where visitors of many kinds are frequently in residence. The " Guests of British Ants " have recently formed the subject of a work by Donisthorpe, and amongst them spiders take a notable place. Spiders that associate with ants may be divided into three groups :

(i) Spiders that always live in ants' nests, where they are passively tolerated.

(ii) Spiders that hunt and prey on ants and are therefore found outside and near the nests.

(iii) Spiders which mimic ants and live near their nests.

These groups are not absolutely distinct, for a spider may belong to two of them, but they broadly indicate the nature of the relations between the spiders and the ants.

The commonest European spider in the first group is the little *Thyreosthenius biovatus*. This spider may be found at any time and in any place in the nests of the red ant *Formica rufa*. Spiders in this group do not feed on the ants. They use the ants' nest as a shelter and they eat small insects of various kinds which are also sharing the same nest. The ants themselves pay no heed to the spiders. On one occasion an ant was seen to pick up a spider in its jaws, but it soon dropped it, and the spider ran away unhurt.

Spiders of the second group are not very numerous. The commonest British examples are the six-eyed spider *Harpactes hombergii* and the pretty little *Asagena phalerata*. These spiders may also be found in neighbourhoods not inhabited by ants.

The group of ant-mimicking spiders has been described above. As an illustration of the closeness of the mimicry it may be recorded that on one occasion Donisthorpe captured the spider *Micryphantes beatus* in the belief that it was an ant ; while of an association of the spider *Linyphia furtiva*, the workers of the ant *Formica sanguinea* and the larvae of a bug, *Aludis calcaratus*, he writes, " I certainly did not know which I was bottling."

It is well worth remembering that ants' nests are among the best places to search for rare spiders, and that many species have been discovered in this way.

Social Spiders

The adoption of a communal life as a means of avoiding attack must, of necessity, be rare among cannibals such as spiders ; nevertheless a few instances are known.

Stegodyphus is a genus in the Eresid family. The Mediterranean members have ordinary habits ; but there are species of the genus in Africa and elsewhere which live in societies. Three gregarious species are found south of the Zambesi—*Stegodyphus africanus*, a northern type reaching Mashonaland, *Stegodyphus gregarius*, found in Natal and also common in Ceylon and the East Indies, and *Stegodyphus dumicola*, which extends from Mashonaland to Cape Colony.

The society begins as a single cocoon, protected by a silk chamber about the size of a walnut. When the young hatch, they gradually enlarge this and at the same time construct a snare or web above it by merely crawling about and leaving a network of draglines behind them. These building operations go on and on unchecked, until the nest in the middle is as large as a football, and is traversed by galleries and passages leading from chambers within to the web above. The web is now many yards in extent and may cover a whole tree—the prickly pear is a favourite haunt—so that the leaves are scarcely visible. In winter the upper web is considerably thickened.

The nest includes from forty to one hundred spiders, and it has been found in some nests that there are seven times as many males as females. The females do all the spinning required for the repair of the web and nest; the males think of nothing but feeding and courtship, often interrupting the work of the females with their importunities. When an insect strikes the web, numbers of spiders hasten to the spot and join in the capture. When the prey is killed, the spiders together drag it nearer the nest, though they take nothing inside. All feed on it together. The instinct to drag objects from the web to the neighbourhood of the nest is firmly implanted, and many a piece of useless rubbish is laboriously carried down. Even drops of water are picked up and treated in the same way.

Among some species at least, in-breeding appears to be the general rule. Mating occurs in the web and the eggs are laid in chambers in the nest. As the younger generation grow up, the old ones die or go off to found another colony.

Some of these webs harbour a guest in the form of a small moth, *Batrachedra stegodyphobius*. The larvae creep about the web and are, for the most part, unmolested by the spiders, although they finish up the food which the spiders have caught. The moths into which they develop continue to live in the colony, although why they should do so is still something of a mystery.

Simon has recorded another instance of communal life in *Uloborus republicanus*, a spider found in Venezuela and Cuba. A peculiarity of this society is that the males generally live all together in one corner of the mass of webs.

The Enemies of Spiders

The natural enemies of spiders fall into three groups. In the first group come the many animals whose usual food consists of insects and which do not refuse to eat spiders when they get the chance. In the second group come the Ichneumon flies, and in the third the wasps.

Birds are the most active members of the first group.

Warburton has recorded the sight of a hedge-sparrow "going conscientiously over a trellis-work and picking out all the spiders from the nooks and corners." In one recorded instance of the contents of a bird's crop, spiders were found to compose eight per cent. In addition to this, spiders' cocoons are often used by birds as lining for their nests.

This group will also include harvestmen, toads, lizards, and all the insectivorous mammals, even monkeys, as well as the spiders themselves, for they often prey on one another.

The Ichneumonidae, which compose the second group, are a huge family of Hymenopterous insects which threaten spiders in two ways. Nearly all ichneumon larvae are parasites, and the egg of the ichneumon may be laid either in the spider's cocoon or in the body of the spider itself.

In the former case the egg of the ichneumon hatches before those of the spider, and the larvae use the spider's eggs as food. The complex architecture and the hard coat of grit which characterise some of the cocoons of spiders are no doubt adaptations which tend to prevent the ichneumon from successfully placing its egg, but in spite of these precautions, few cocoons are really ichneumon-proof, and a large proportion will be found on examination to be sheltering these parasites. It is probable that many species of ichneumons in all countries lay their eggs in the cocoons of spiders.

Other ichneumons lay their eggs on the body of the spider itself. Members of the web-spinning families seem to be the victims usually chosen, and it appears that the spider is demoralised by the approach of the ichneumon fly and offers no resistance. The egg is placed by the ovipositor just below the skin on the "shoulder" of the abdomen, and in time the small larvae hatches and clings to the same spot. In the summer it is seldom that one passes a week's collecting without coming across a spider carrying the burden of the small white "worm." If these spiders are kept alive in cages they continue their usual

habits for some time, but, as has long been known, they do not cast their cuticle. It may be that the demands of the parasite prevent the host from increasing in size and so render moulting unnecessary, or, as is perhaps more possible, the subtle relation between the two organisms includes the production of a toxin which prevents moulting. However this may be, the death of the spider, even in the presence of food and drink, seems to be unavoidable. The writer has kept many parasitised spiders and plied them assiduously with all the food they would take, but never has he so far succeeded in tilting the equilibrium the other way and enabling the spider either to get rid of the larva or to stave off an early death.

Soon after the death of the spider, the ichneumon larva pupates and its beautiful little cigar-shaped cocoon may be found in the cage (Fig. 74). The imago appears about a fortnight later and, in the circumstances mentioned above, soon dies because it can neither feed nor escape from the spider's cage.

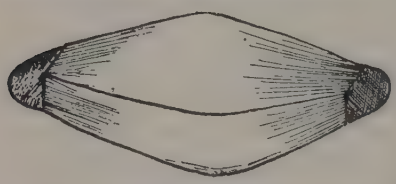


FIG. 74.—Cocoon of Ichneumon from spider's web.

Wasps form the third group. Social wasps occasionally use spiders as food for their larvae. They catch the spider, sting it to death, and carry it to the nest, where it is cut into pieces and fed to the young.

The solitary or fossorial wasps are, however, the spider's chief enemies, and it is probable that they are responsible for a greater number of casualties among spiders than all other causes taken together.

The family Pompilidae, the largest and most important of the group, is spread over almost the whole of the world, and all its members make spiders the chief food for their larvae. Their custom is to excavate a hole in the earth, store it with spiders, deposit an egg, and then seal up the hole. By the exercise of one of the greatest marvels of instinct, these wasps sting the spiders in the nerve ganglion

of the cephalothorax. This prevents the spider from struggling, which might kill the wasp grub, and also from decaying, which would render it unfit for food. These paralysed spiders have been known to live for seven weeks, during which they were unable to feed or to make any movement whatever.

Sometimes only a single spider is thus imprisoned, but sometimes there are many. The wasps show the greatest energy in attacking even comparatively large spiders. They try to come upon them unawares, and, grasping a leg, to jerk them suddenly from their burrows or webs. Thus thrown down, the spiders seem to offer but a feeble resistance, and wasps of the South American genus *Pepsis* can overcome *Eurypelma hentzii*, one of the largest known spiders. Wasps of the family Sphegidae also use spiders on occasions for the same purpose.

There is little doubt that the protective adaptations described earlier in this chapter, as well as the great fertility of some spiders, are largely necessitated by the persecution which spiders suffer at the hands of wasps. Peckham has recorded how in a single haystack some six hundred wasps' cells were constructed in the space of six weeks, and each cell contained about ten spiders. Some wasps, such as *Sphex cyanea*, store twenty to thirty spiders in a cell. A similar account of the immense slaughter of spiders by wasps has been written by Hingston.

Another description of a different character has been given by Montgomery. The wasp *Boeus montgomeryi* is a tiny insect, little bigger than the spiders' eggs ; it bores its way into the cocoon and can be seen, with a microscope, piercing the eggs with its ovipositor as it crawls about. Not all the eggs of a cocoon were thus infected, and if hatching occurred in a closed space, the luckier spiders, which hatched at about the same time as the wasps, ate their unwelcome visitors.

Longevity

After this consideration of the enemies of spiders, which almost make us wonder how any spider ever survives at all, it becomes of interest to inquire what age spiders are capable of attaining. Such an inquiry has, as a matter of fact, very little biological significance, since death from old age is practically unknown in Nature. The normal end to the life of an animal does not come as a climax to that gradual slowing of all the body's functions which men call ageing ; it comes when first the creature fails to get out of the way. Such a death we are accustomed to call violent, but, biologically speaking, it is natural and usual.

None the less the interest remains, for if the survival of the individual is due to a succession of escapes from death, Chance may occasionally permit these escapes to continue.

The majority of spiders are hatched in the autumn or spring, mature during the spring or autumn following, and die in the winter. They are creatures of a single season, whose life-work is done when they have spun their egg-cocoon. Some, however, survive the winter by " hibernating " in hidden silk-lined cells. Blackwall many years ago showed that the six-eyed spider *Segestria senoculata* can live four years, and Fabre has given reasons for believing that the wolf-spider *Lycosa narbonnensis* reaches the age of five.

More recently the deaths have been recorded of two house-spiders, *Tegenaria derhamii*, which had been kept and fed by Dr. Oliver of Bradford. One of these had been in his care for five, and the other for seven years. We may take these as quite exceptional ; probably five years is the limit for all those spiders that survive more than a single season.

CHAPTER IX

THE DISTRIBUTION OF SPIDERS

THE study of the present-day distribution of any group of animals is always of interest and importance, for the facts of distribution shed light upon the past history and evolution of the group.

The extent to which a race has spread over the surface of the earth must clearly be dependent in no small degree upon the methods of dispersal of which it has been able to avail itself. Thus flight, or a power of sustained travel on foot, or an ability to remain alive in crevices of floating logs, may all play a part in carrying different types away from their centres of origin.

It is obvious that in the spread of the race of spiders the well-known gossamer habit must have played a prominent part.

GOSSAMER

Gossamer-making is not only well known, but universally attractive. Be the spider, in popular esteem, never so dirty, cruel, or blood-thirsty, there is nothing but admiration, and even poetic praise, for the small aeronaut.

We have already tried to trace the origin of much of the spider's spinning-work from the habit of leaving a dragline behind it, and it seems not unreasonable to imagine that the use of a single thread for aerial migration arose from the same beginnings. The spiderling to-day is, as we have seen already, different from its elders in being positively heliotropic and negatively geotropic for a fleeting period of its young life. Almost as soon as it is free from

the cocoon it must guard against overcrowding and consequent fratricide, and it avoids these calamities by its obedience to the instinct of dispersal.

Its first impulse is, therefore, to climb as high as possible on the plants or other objects about it. When it has reached the top, it turns its head to the breeze and raises its abdomen. The spinnerets secrete a drop of silk which the slightest breath of air will draw out into a thread, or sometimes into two diverging threads. There is no doubt that movements of the air, even those too slight to be noticeable to ourselves, act on the silk droplet in this way, for it has been found that spiders, unable to set sail in a room in which door and windows were closed, will immediately do so on the admittance of a slight draught. When the streamer is pulling with a sufficient buoyancy, the spider lets go with all its eight legs at once and launches forth on a voyage which may carry it yards—or miles.

The most remarkable feature of this process is its swiftness. It sounds, when described, as though it were a matter of climbing, turning, spinning, and waiting, whereas in actual fact it is often far otherwise. It is one of the many surprises of spider-study to have a small spider run up one's finger and apparently run straight on into the air. The turning, spinning, and setting forth may be, in certain circumstances, all but simultaneous.

There are two particular instances of gossamer spiders in well-known literature, which are often quoted, and which happen to illustrate two important features of this method of dispersal.

The first is Darwin's record of their arrival on the *Beagle* when sixty miles from land. We have mentioned this already in a former chapter: it is of interest as illustrating the great distances to which migrating spiders may sometimes be carried. McCook records another occasion, in which the ship upon which the spiders embarked was upwards of two hundred miles from land, and the little creatures, after a short rest, set sail again.

Both Captain Scott's Antarctic expeditions, in the

Discovery and the *Terra Nova*, visited the remarkable island of South Trinidad, and made collections of spiders there. The island lies in the course of the south-east trade winds, about lat. 20° S. and long. 29° W., and there is little doubt that it has received its spider population by gossamer migrants coming from great distances. The spiders which frequent mountains, where they often reach very considerable altitudes, have usually made the ascent in a similar way.

The second instance is that described by Gilbert White, in Letter LXV from Selborne. A prodigious shower of flakes of silky web fell all day (September 21, 1741) over an area which was, at the least, a triangle with sides some eight miles in length.

So great a quantity of gossamer is not a common occurrence in England, and is really a different phenomenon from the ordinary migrations. In parts of America, however, it is said to be an annual occurrence. It is probably associated with unusual weather conditions, which in this particular instance White describes as "cloudless, calm, serene, and worthy of the South of France itself." This, in the first place, provokes a general awakening into activity of all the small spiders hiding and resting near the ground, and, secondly, raises a convection current of warm air. In these circumstances, the spiders are constantly producing webs and threads among the grass, and these threads are as constantly wafted away by the upward currents. Many of these threads get tangled and crossed with others, so that much of the floating silk consists of flakes or rags, rather than the single threads of migration. White describes some as nearly an inch broad, and five or six inches long. But only a small proportion of these floating webs are inhabited by spiders, and it is probably quite incorrect to regard the days on which these phenomenal showers occur as days of great migration. They are certainly days of great activity among spiders, for it is invariably true that much gossamer in the air is accompanied by much business among spiders on the ground. Gilbert White's settlers had

constantly to "lie down and scrape the incumbrances from their faces with their forefeet." The fact is that both the awakening of the spider populace and the floating of their silk into the air are prompted by the peculiar state of the weather, but the frequent entanglement of the threads prevents many aeronauts from making a successful start.

It is a rather common belief that the spiders whose migration threads are seen floating across the fields in spring and autumn belong to one species—the "gossamer spider"—or at least to one family, whose members have made a speciality of the habit. This is not so. It is, however, generally true that the habit is confined to spiders which do not avoid the light and the warmth of the sun—that is to say, to the web-spinning, the hunting, and the jumping families. The spiders which wander about at night, which live in burrows, and which hide themselves away under stones, do not, as a rule, practise the habit to any great extent.

The necessary result is, therefore, that the light-loving spiders are very widely spread over almost the entire globe. Their distribution is much more nearly that of a creature able to fly than that of a terrestrial animal, as a spider must properly be considered. When, however, we look a little more closely at the distribution of these ubiquitous spiders, we discover facts of great interest, not free from difficulty. They show how much is still to be discovered about the conditions of existence among invertebrates.

Spiders' Stations

The statement that spiders may be found everywhere is true in a general sense, but it is not always the same spider!

Malacologists have long been familiar with this distinction. Many species may be represented over a certain area, yet each is to be found in its own particular station. A given species may perhaps be confined to a few square yards, within which it is abundant, while it is useless to

look for it elsewhere. Seekers after spiders meet with exactly the same state of affairs.

In most localities in England, about a hundred species of spiders can be found without much difficulty in a season or two. Several of the commoner species are found in the sheds and stables at home, and occur again, but with striking additions, in the conservatory and greenhouses. Running in the open fields are many wolf-spiders, but to complete the survey of this family alone, the banks of

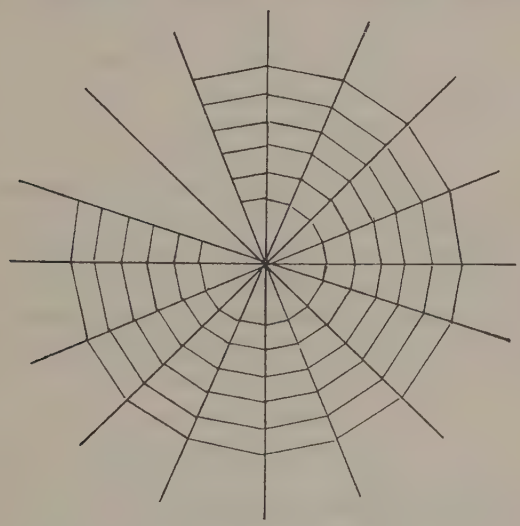


FIG. 75.—Web of Zilla.

rivers and streams, the sandhills and the seashore must also be searched. An entirely different bag is the reward of beating and sweeping the hedges and lower branches of trees. A multitude of the smaller fry are taken by sifting dead leaves, pine-needles, moss, and grass roots. Quarries harbour others, heather conceals many seldom seen elsewhere, others again are hiding beneath the bark of trees. Many of the rarest are found under stones loosely bedded in the earth; one species, and only one, lives in fresh water, a few are guests in the nests of ants, and finally,

there are some spiders that do not live much below the thousand-foot contour.

All this may be familiar, but its significance begins to appear when the distribution of the different families among the diverse habitats is realised. Let us take a few examples to illustrate this big subject.

The genus *Zilla*, which spins an orb-web with one isolated radius (Fig. 75), is represented in Great Britain by three species, one of which, *Zilla stroemii*, is rare, while the other two, *Zilla atrica* and *Zilla x-notata*, are exceedingly common, being both numerous and widely distributed. These two species are so closely allied that the separation of the two females, lying on the laboratory bench, is a matter demanding the greatest care. But in collecting them it is found that *Zilla atrica* is taken out of doors, from bushes and shrubs, while *Zilla x-notata* lives in the angles of doorways and window-frames, both inside and outside the house, but never far removed from buildings. It is quite hopeless to look for either of these spiders in the place occupied by the other, and the problem under discussion is emphasised by the very close structural resemblance between the two species.

Choice of Environment

Two hypotheses might be framed to explain the facts: either that there is no connection between structure and environment, or that each spider receives from the station it adopts, and would lack in the one it abandons, some advantage in the struggle for existence. The former hypothesis is clearly untenable, for its acceptance would practically amount to a denial of the adaptation of the organism to the environment. If this were so, every spider, and indeed every animal, could live everywhere.

We are therefore driven to assume that each of these two closely allied spiders must receive from the environment it has chosen some benefit which the other has not. This benefit must be such that it is not appreciated by a

structural difference, for such differences do not exist, or, if they do exist, are not yet recognised.

The alternative interpretation is that the environmental differences may be correlated with differences in habits. This is quite conceivable. It may be that it is a difference in activities, or in response to external change, that confines the two species to their separated spheres. The hypothesis is capable of being tested by a sufficiently intensive study and comparison of the habits of the two species, a study which would be almost sure to yield interesting results. Although it is impossible to suggest a lack of connection between habits and structure, it is none the less possible that the reactions of two spiders might diverge without producing a corresponding and obvious difference in their structure.

The relationship between the spider and its environment is threefold, inasmuch as the latter provides the former with (i) food and water; (ii) concealment from enemies; (iii) warmth and shelter. If we apply these considerations to the case of the two *Zillas*, we can easily rule the first two out of court. For, as has been noted in an earlier chapter, a spider will feed upon anything that it can catch. To suggest, as some have done, that the distinction is due to each spider's habit of specialising in some particular brand of fly, shows unfamiliarity with the ways of spiders. Both environments, too, supply all the concealment necessary, for the spider rests in a silk retreat of its own making, which may be under a leaf or in the window-corner. From any of these points of view, therefore, it is exceedingly difficult to see why a window-frame should be better than a bush.

Influence of Temperature

The very obvious suggestion that *Zilla x-notata* requires a higher temperature for its comfort is negatived by the fact that it as often spins outside the window as inside, and as often in unwarmed sheds as in our houses. Yet the

actual temperature may not have so great an influence as the variations to which it is liable.

Exposure to winds and to changes in humidity must be much more severe on the bushes than in the comparative shelter of the side of a house, and the range of temperature, or difference between the daily maximum and nightly minimum, is well known to be very much less in the former situation.

It may be assumed, then, that spiders are very sensitive to changes in the physical conditions of their environment, that there is an optimum, from which any departure is most unwelcome. The malacologist would say the same in explanation of the distribution of molluscs on the shore.

There is ample support for the belief that *change* in the physical conditions is more potent than the actual condition itself. The occurrence of spiders on mountains affords convincing evidence. We know, too, that comparatively small changes in concentration of hydrogen ions in a fresh-water pond produce remarkable and seemingly disproportionate changes in the animal and plant life.

Response to Physical Changes

Experience in collecting spiders tells the same story, for many species are localised within exceedingly narrow boundaries. It can only be sensitiveness to change in the physical condition which is responsible for such confined stations.

For example, in a large wood near Malvern, where the writer often collects, the beautiful *Epeira pyramidata* (Fig. 76) is to be found. At the right time of year a couple of dozen may be seen in half an hour—all within a space of a hundred yards. Here the spider is abundant, yet nowhere else in the country round and nowhere else *in the same wood* has a single specimen ever been seen.

A very striking instance is reported from Litchfield by Carr. The spider *Agyneta ramosa* is common under a clump of bushes a few square yards in extent: it has

never yet been found elsewhere in the whole world, not even under the apparently similar clumps which are plentiful in the immediate neighbourhood.

The sudden disappearance of spiders from a haunt confirms what may perhaps be called the individuality of distribution. Many jumping-spiders, for example, are but fleeting inhabitants of their neighbourhood. It is possible to find ten or twelve individuals within an hour at a place where, a week later, a day's search may be quite unrewarded.

Our belief is, then, that although some spiders are ubiquitous, there are many others which react strongly to change in the physical environment. This must imply susceptibility of internal organisation and need not necessarily be expressed in marked external features. It is, therefore, possible to find, within the limits of a single genus, such striking differences as that of the two *Zillas* considered above. These two stand at extremes of the scale and it is only reasonable to look for instances where a gradation of habits occurs—showing us, perhaps, the steps by which the process has come about. It is very easy to find examples which illustrate this.

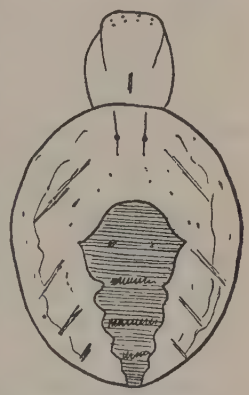


FIG. 76.—Epeira pyramidata. The abdomen is bright yellow with brown marks.

Four species of the genus *Tegenaria* are common in Great Britain, occurring in the situations mentioned below :

1. *Tegenaria derhamii.* Nearly always indoors.
2. *Tegenaria parietina.* Usually indoors, sometimes outside.
3. *Tegenaria atrica.* Sometimes indoors, very often outside.
4. *Tegenaria silvestris.* Nearly always outside.

There are here, therefore, what may be described as

four consecutive terms of a series, an illustration of a gradual transition from an outdoor life of comparative variability to an indoor life of comparative constancy of physical conditions.

Another example is provided by the genus *Lycosa* of the wolf-spiders, eighteen of which are found in Britain. Eight of these are widely distributed, and of these eight only one is arboreal and is always to be found on the branches of trees or shrubs ; one is riparian, living among river shingle, and one is sylvan, and prefers the shade of the woods.

The fact is that the system of classification which we use stresses architectural similarity which is only an external, and therefore a partial, expression of the relations between species. Thus they may conceal differences in the manner of life which are essential characteristics of the animal as a living organism.

We have to realise that while we can perceive these structural details, we remain ignorant of their active utility. As mammals, we are provided with a regulating system which tends to stabilise our internal environment and make us in some measure indifferent to external change. We have only begun to realise that, for the cold-blooded invertebrate, changes in temperature, alkalinity, humidity, and electrical state may have a very different significance.

Ritter has lately pointed out that what is truly characteristic of a species is the way it behaves. This exceedingly significant statement exactly summarises the foregoing considerations of the relation between the spider and its environment. We may look upon it, as an analogy, by comparing the life of a spider in its environment to the turning of a key in its lock. Each ward of the lock represents a physical condition, temperature, humidity, wind velocity, and so on. If a ward is altered, the key no longer turns ; and similarly if a condition changes, a species no longer inhabits a particular environment, or at least will not be able to do so as successfully as before. But clearly, a variety of the species might be better able to survive under

the changed conditions, and here is the raw material for producing a step in the evolution of the spider-race.

Geographical Distribution

Let us pass from the parochial to the continental distribution—the geography of spiders. This subject may be looked at in two differing yet complementary ways, by considering either the localities favoured by the species of certain distinct groups or the spider population of different types of environment.

It is only in a comparatively small number of cases that the distribution of any group has been worked out in detail. Chief among these stands out the sub-order Mygalomorphae, the subject of a masterly paper by Pocock. Trap-door spiders lend themselves particularly well to the study of distribution, for they seldom migrate on gossamer-threads. Many of their newly-hatched young are as heavy as the adults of most other spiders and are too big for this mode of transport.

Pocock points out that in very early Tertiary times the primitive trap-door spiders arose in Eastern Asia and spread thence in four directions :

1. South-east to Australia and New Zealand, where a very primitive type, *Hexathele*, still survives. The ancestor of its near ally, *Scotinoecus*, crossed from here to South America.

2. South-west to India, Madagascar, and tropical Africa ; from here to South America.

3. North-west to the Mediterranean.

4. North-east to North America.

The later forms have arisen from these four centres and spread all over the world, except into the cold northern region. The only genus reaching temperate climates is *Atypus*, the representative found along the south coast of England and Wales.

The chief peculiarity of the distribution of existing Mygalomorphae is the persistence of a distinct Mediter-

ranean region, north of the Ethiopian and south of the great mountain ranges of Europe. In 1903 twenty-two genera were known from this region, more than half of them being peculiar to it.

The Distribution of Liphistiomorphae

These results are in striking contrast to the distribution of the sub-order Liphistiomorphae, which in Tertiary times was the dominant type of spider throughout the world. To-day these spiders have no survivors in America, North or South. The small number of species which have managed to persist are almost entirely confined to Penang and Sumatra, and, since their unusual form would attract the attention of any naturalist, it is most probable that they occur nowhere else. This surprising fact suggests that in the East Indies alone of the habitable world, *Liphistius* and its allies have found an environment in which they could persist unchanged for geological ages. It is quite in accordance with this that Sumatran fauna is very distinct from that of Java, across the narrow Straits of Sunda. For example, a species of elephant found in Sumatra does not occur in Java, while an ape, one of the Gibbons (*Siamanga syndactyla*), is peculiar to that island.

The Distribution of Arachnomorphae

The sub-order Arachnomorphae is too widely spread to yield valuable results when taken as a whole. The Peckhams published, about twenty years ago, a table showing the distribution of the families of spiders among the six regions defined by Alfred Russel Wallace—Ethiopian, Oriental, Palaearctic, Australian, Nearactic, and Neotropical. Nineteen of the 35 Arachnomorph families then recognised are represented in all of these regions. At the other extreme are five families represented in but one region only—Psechridae in the Oriental, Hadrotarsidae in the Australian, Platoridae and Senoculidae in the Neo-

tropical, and Ammoxenidae in the Ethiopian. The explanation of this is probably similar to that given for the Liphistiomorphae. The number of genera from the widespread families having a discontinuous distribution forms an extremely small proportion of the whole, and may well be supposed to be the survivors of a more general type whose intermediate species have become extinct.

Spiders on Mountains

The adaptability of spiders, combined with that insurgence which characterises all living creatures, explains their representation in all situations except in the depths of the sea. We may select for short considerations the following four localities :

1. Mountains.
2. The Polar Regions.
3. Oceanic Islands.
4. The Sea-shore.

Of special interest are the spiders which are found at great altitudes, for they have not only reached places which the majority of their kind never attain, but they have also to withstand exposure to temperatures and winds which never affect their relatives in the plain. It is therefore unfortunate that few mountaineers are arachnologists, and few arachnologists mountaineers.

Prominent among the exceptions is Dr. Jackson, who has collected many rare species from the mountains of both Wales and Scotland. The main characteristic, which seems to be shared by all the British mountain species, is small size. Nearly all of them belong to the family Linyphiidae. Their habitat is generally one that will afford as much protection as is possible in the circumstances, and their usual dwelling-place is under a stone, almost embedded in the earth.

A number of related species of spiders have been collected from the mountains of central Europe, and

recently attention has been directed to the subject by the discovery of spiders on Mount Everest itself.

Far above the highest plant, which grew at an altitude of 18,000 feet, small black spiders belonging to the family of jumping-spiders were found, hopping among the rocks and hiding under the stones in such places as were swept bare of snow by the wind. They reached a height of 22,000 feet, at which altitude they were not only in the proud position of being the highest permanent inhabitants of the earth, but seemed to be alone in their isolation. No other living thing has been found to share their loneliness. There is nothing but rock, snow, and ice. What they get to feed on is a mystery.

Some very interesting observations made by Hingston on Mount Everest in 1924 throw light on the conditions in which these spiders have to live. He compared the temperature of the air with that under a stone at a height of 17,000 feet on 21st May. The results were :

	Under stone.	In air.
Maximum temp.	39° F.	56° F.
Minimum temp.	27° F.	12° F.
Range of temp.	12° F.	44° F.

This shows that by seeking the shelter afforded by a stone, the spider obtains far more uniform conditions than it would experience elsewhere. It is also important to realise that the temperature of the air does not vary nearly as much as that of the surface of the sand in exposed places. This is shown by a set of observations taken at the Base Camp at 16,500 feet on 20th May.

	Temp. of sand.	Temp. of air.
Maximum temp.	96° F.	55° F.
Minimum temp.	2° F.	11° F.
Range of temp.	94° F.	44° F.

It is clear that the spiders are seeking the most uniform set of conditions available. They may be found in April, dormant inside small snail shells, but it is noteworthy that as summer comes they are among the first to shake off their winter's sleep and may be seen running about on the moist earth at the very edge of the retreating snows.

Spiders of the Polar Regions

The hardy spiders from great heights naturally suggest comparison with those from the polar regions where conditions are of somewhat the same degree of severity.

No spider has yet been found in the Antarctic Continent. A trawl, recorded in *Scott's Last Expedition* (vol. ii, p. 94), was made by Capt. Campbell off Cape Adare, and is reported to have yielded " one sea-louse, one sea-slug, and one spider," but this must refer to one of the Pycnogonids, which are often called sea-spiders.

From the sub-antarctic islands, however, a number of very interesting spiders have been recorded. The islands of Macquarie, Auckland, Snares, Campbell, and Bounty lie between latitudes 47° S. and 54° S., and may be supposed to represent the remains of an ancient connection between South America, Australia, and South Africa. The present distribution of other animals suggests very strongly that such a connection must have existed in the past; hence the value of a study of all the fauna of these islands.

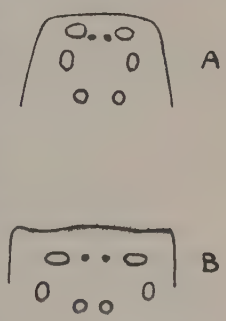


Fig. 77. — Antarctic Eye-Pattern. A, Myro hamiltoni. B, Rubrius nummosus. After Hogg.

All of these sub-antarctic spiders resemble the mountain species in being of comparatively small size, simple form, and sober colours. The bright hues and highly evolved bodies, common in the hotter lands where food is plentiful, are altogether lacking.

Orb-spinners, wolf-spiders, and jumping-spiders, which are found all over the world, are represented among the sub-antarctic species, but in addition to this a single group, the Cyboeeae, of the house-spider family, Agelenidae, stands out pre-eminently as definitely Antarctic. A quite disproportionate number of the island spiders belong to this group, which is represented over the whole distance between South America and South Africa. There seems

also to be an Antarctic eye-pattern. In northern and tropical forms it is rare to find the direct eyes smaller than the first indirect eyes, but such an arrangement (Fig. 77) is comparatively common in spiders of more than one family from the far south.

The Arctic regions are in every way different from the Antarctic. For the South Polar Continent is a land mass, mostly of great altitude, isolated from the rest of the world by immense stretches of storm-swept ocean, while in the north there is no continent, only a frozen sea-basin, almost surrounded by land. The conditions at corresponding latitudes are therefore far less severe in the north than in the south, and the pole-ward spread of animal life is therefore greatly facilitated.

Thus, within the Arctic circle are lands of comparative fertility, supporting the Esquimaux and the Samoyeds, with their herds, and producing flowering plants. In these circumstances it is not surprising that Arctic spiders are plentiful and have long been known.

Thorell had described spiders from Siberia and north Norway more than sixty years ago. Most of the Arctic expeditions from those that sought the North-West Passage to the recent parties of scientists who set out from Oxford, have brought back collections of spiders.

The predominant Arctic type belongs to the Linyphiidae, the same family of midgets as that represented on the highest mountains of Britain. Many other families, however, include Arctic representatives—there are, for example, about a score of Arctic jumping-spiders. This is not surprising, since access to Arctic regions is comparatively easy. All share the general features which we have already seen to characterise the spiders of a cold environment—small size, simple form, and sober colour.

Spiders of Oceanic Islands

The spiders of oceanic islands form two groups. These are the endemic or original inhabitants and the later

immigrants; and nearly every island includes both kinds.

Madeira is probably the oceanic island whose spider fauna is best known. In 1892 Warburton compiled a list of 64 species known from the Madeiras, over half of which were taken to be endemic. Most of the rest probably arrived on gossamer threads, and some, such as *Argiope trifasciata* and *Pholcus phalangioides*, were probably introduced by man. A few may have made the journey on floating objects.

Some spiders of the Falkland Islands and of the Montebello Islands have been described by Hogg. In both instances a big proportion of the collection consisted of members of the orb-weaving family Epeiridae, which is spread throughout the world, and most of the remainder belonged to families whose members are well known to be conveyed by wind. It is thus clear that spiders are not suitable subjects for providing evidence as to the past history of oceanic islands.

Spiders of the Sea-shore

The littoral region, so prolific in other forms of life, is only rarely inhabited by spiders; but the spiders which are found there are, necessarily, of great interest.

The first to be discovered was *Desis martensi*, found by Dr. Martens at Singapore in 1861. He described its habit of concealing itself in a retreat impermeable to water at high tide, and of coming out at low water to hunt Isopods and other small creatures.

In 1877 a fuller account was given by Pickard-Cambridge of an allied species, *Desis* (*Robsonia*) *marina*, caught in the tidal pools off Cape Campbell, New Zealand. The rocks of Cape Campbell are full of holes bored by molluscs, and in these the spiders make their retreats and spin their cocoons of eggs. They close the mouth of the hole with a web, which is water-tight, the rocks being covered by the sea at high tide. The spider swims in the water of the pool,

just as our English water-spider swims in ponds, and there catches its food, which consists of small fish and crustaceans. The original account says: "When a small fish is placed in a bottle of water with one of these spiders, the latter will attack it at once, driving its long sharp fangs into the fish near the head, and killing it instantly."

Since 1877 six other species of the same genus have been discovered from Samoa, Victoria, and South Africa. The distribution of this genus is of particular interest, because its restriction to the shores of Africa, Australia, and Eastern Asia furnishes another example of the similarity between the fauna of the Australian and Ethiopian regions, and supplies another item of evidence in favour of a former land connection between the two continents.

Three of these remaining species are worth noticing: the first, *Desis Kenyonae*, of Victoria, has a blue abdomen and a red cephalothorax—an unusual selection of colours; the second, *Desis tubicola*, lives deep down in rocky holes or in the calcareous masses made by a marine worm *Tubicola*. It is a soft and delicate creature, unable to dive and unable to live long in a dry box. How it survives among the breaking waves or how it feeds is a mystery. The third, *Desis crosslandi*, is a species from Zanzibar. As a rule the African forms are somewhat distinct from the Malayan, and the Australian ones are intermediate, but this species is of the Malayan type. This would imply that north-east Africa got its species of *Desis* from the same source as Malay, and that the southern forms are the results of a later modification.

The family Agelenidae, to which *Desis* belongs, contains some other semi-marine species, such as *Muizenbergia abrahami* of Muizenberg, South Africa, and *Desidiopsis racovitzai* of the Mediterranean. But the other families are not without their littoral representatives.

In 1894 a semi-marine spider was discovered in England, and described under the name *Lycosa purbeckensis*. It belongs to the family of wolf-spiders, and quite lately Bristowe has described its habits. The spider has been

found at several places on our coasts, where it lives among the plants that grow between the tide marks. At low tide it hunts for food—any of the insects or other small creatures which abound in such haunts. As the tide rises, the spiders crawl down the stems of plants, carrying with them a bubble of air, entangled in the long hairs with which they are covered. At the roots, they rest in security. Experiment has shown that the air which accompanies them will last for quite ten hours. Although they can run on the surface, they seldom do so, being more comfortable below it. They are, however, unable to dive, but must crawl down stems of plants if they are to break the water surface.

It is a far cry from the Lycosidae to the tiny black Linyphiidae, yet, different as are the habits of typical members of the two families, there are a few of these midgets that live in the same littoral region. Bristowe noticed three of them in the Isle of Wight accompanying his wolf-spiders ; others have occurred on the Irish coast, and the writer has found yet more in Pwllheli harbour.

There, among the seaweed and coarse green vegetation, the little spiders are plentiful, spinning delicate webs close to the ground. When taken home and dropped into a tumbler of sea water, the spiders float on the surface. If pushed under, they slowly sank, upside down, the lungs covered with an air bubble, the legs outstretched. With the hind legs, they held on to any object capable of affording anchorage, and so remained content for several hours.

To complete our catalogue we must include *Amaurobioides* of New Zealand and *Uliodon* of Madagascar, which are both members of the family Clubionidae, and two Malayan coast spiders recently discovered by Abraham. One of these, *Diplocanthopoda marina*, is a jumping-spider ; the other, which feeds on marine worms, is *Idioctis littoralis*, the first known marine Mygalomorph spider.

The spiders of the sea are not, therefore, members of a single pelagic family. Like the spiders of mountains and caves they are wanderers from beaten paths, derived from

several parent stocks ; originally-minded spiders, who have colonised a new environment. They illustrate the insurgence of life ; that universal will to live which seems to inspire all creatures. As Goethe said : " Animals are always attempting the almost impossible—and achieving it," and spiders have not hesitated to go up to the hills or down to the sea and seek their livelihood on the edge of its waters.

CHAPTER X

THE COURTSHIP OF SPIDERS

ACTIVITIES of courtship, or preliminaries before mating, are well known to biologists, and have been described by observers of nearly every kind of creature from mankind downwards. Spiders supply many examples of these performances, and also provide good material for the discussion of their significance. Indeed, it is probable that on this line the study of spiders may make a very real contribution to the study of animal behaviour.

THE COURTSHIP OF JUMPING-SPIDERS

In this matter of courtship one family of spiders stands supreme. This is the family of jumping-spiders, or Salticidae. Our knowledge of their " dances " is due almost entirely to the patience and enthusiasm of Dr. and Mrs. Peckham, who published their well-known papers on the subject nearly forty years ago. With a few isolated exceptions, it is only within recent years that courtship among spiders has again attracted attention, and lately work on the subject has been done by Gerhardt in Germany and by Locket and Bristowe in this country. Much of this chapter is indebted to the papers of the latter.

It has been said in an earlier chapter that jumping-spiders are the possessors of keen sight, which enables them to recognise objects at a distance of nearly a foot. Many of the males bear decorations on their legs or palpi, or on both, and sometimes also on their abdomen ; the decorations consisting of tufts of hair or of coloured or

black patches. When a male jumping-spider approaches a female, he seems to recognise her by sight. He then performs a kind of dance before her. He raises his front legs and waves them about, or he holds out the adorned legs of one side and walks round in a circle, or he raises his abdomen into the air. An example may be quoted to give an idea of the complexity of the dance with some species. The classical instance, that of the species *Saitis pulex*, wh ch circled before its mate 111 times, has been quoted so often in zoological literature, that another example, that of a species of *Habrocestum*, is chosen here.

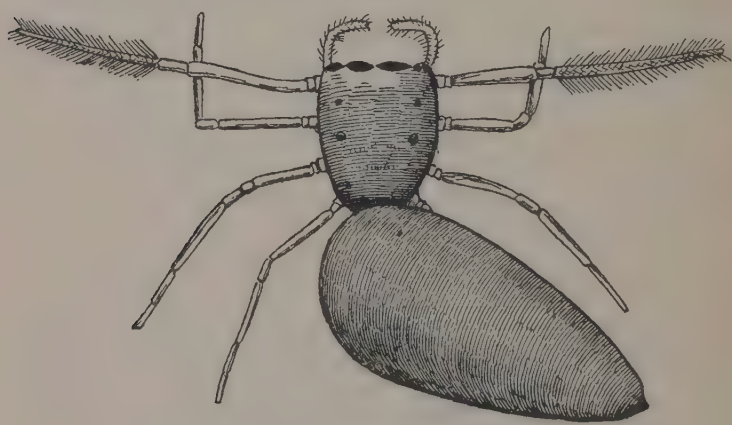


FIG. 78.—Courtship of Icius mitratus. After Peckham.

"He begins to move from side to side, with his handsome first legs pointed downward and somewhat outward, his palpi extended parallel with them and his third legs raised above the first and second, in such a way as to show the apophyses on the patellae. Frequently, in these preliminary movements, he bends the ends of the legs inward, so as to put them into the form of a diamond, meanwhile moving the palpi rapidly up and down. As he approaches the female, he raises the first pair of legs swaying them backward and forward, still keeping the third pair well up, seeming as eager to display them as the first pair. When

he gets to within an inch of her, he lifts the first legs nearly at right angles with the body, giving them a bowed position, with the tips approaching each other, so that each leg describes a semicircle, while the palpi are held firmly together in front. Up to this time he has held the body

FIG. 79.—Courting attitude of Astia vittata. After Peckham.

well above the ground, but now he lowers it by spreading out the second and fourth pairs, at the same time bringing the tips of the third pair nearer the body, and arching the legs over the cephalothorax so that the proximal ends of the tibae nearly meet. Now he approaches her very

slowly, with a sort of creeping movement. When almost near enough to touch her he begins a very complicated movement with the first pair of legs. Directing them obliquely forward, he again and again rotates each leg around an imaginary point just beyond the tip ; when they are at the lowest point of the circle, he suddenly snaps the tarsus and metatarsus upward, stiffening and raising the leg, and thus exposing more completely its under surface. While this is going on with the first pair, he is continually jerking the third pair up higher over his back."

Whatever a jumping-spider does, he is performing a dance which is peculiar to his own species, and other species of spiders will dance in a different way. It is noteworthy that the movements he makes are always such as will best display his decorations. Even if he were conscious of the exact nature of his beauty, as he almost certainly is not, and aware of his precise objects in courting, which is at least questionable, he could scarcely improve upon his display. He behaves just as if he were determined to exhibit himself as conspicuously as possible. The female for her part takes an obvious interest in the proceedings. There is no doubt that she sees the charms that are displayed before her, and watches them intently, for she turns herself so as always to keep the male in full view. Sometimes she brings the business to an end by joining in the dance, the two spiders whirling round together.

The Courtship of Wolf-Spiders

It is clear that a complicated dance of this sort is of interest only to a spider which possesses good eyesight. The only spiders whose eyesight is comparable to that of the jumping-spiders are the wolf-spiders or Lycosidae. Some of the male wolf-spiders have decorations on their legs or palpi, in the form of a brush of black hairs on one or more of their joints. With these ornaments a wide range of courting attitudes is possible.

At the outset, however, it is necessary to point out that

some wolf-spiders show no courtship at all. If a pair of the species *Lycosa pullata* are introduced to one another in a cage, the male usually leaps at the female and mating begins immediately, without any preliminaries whatever.

With other species, however, things do not move so fast. The courtship may consist, as with *Lycosa amentata* or *Lycosa nigriceps*, in waving the palpi in a semaphore-like fashion. Locket thus describes the behaviour of the former species: "The male, on sighting the female, started his usual antics. He raised himself as high as possible on his legs, extended his palpi as indicated above (Fig. 80), withdrew them, and extended them again, the positions reversed. Each time he did this he (usually) took a pace towards the female, and his abdomen quivered now and then. He would often work his way round the female, leaning over in the direction he was going."

Fig. 80.—Courtship of Lycosa amentata. After Locket.

In other species the male may have legs, and not palpi, to display. The common species, *Trochosa ruricola*, raises and lowers its first pair of legs alternately, quivering as they rise, and with the tarsus and metatarsus gracefully and gently waved up and down as they fall. An even more elaborate courtship is that of *Tarentula barbipes* (Fig. 81), in which the cephalothorax is raised by the second pair of legs, while both palpi and first legs are raised into the air together. The legs, in a bent position, are jerked as high as possible and then, trembling violently, are lowered to the ground. Then a step or two may be taken and the process repeated again and

again, until the female ceases to rush at him when he approaches.

The family Pisauridae is not very distinctly related to the true wolf-spiders, and one of its species, *Pisaura mirabilis*, is very common in England. The sense of sight is not quite so well developed, and the male possesses no decoration. His courtship is a far more material business than any of the dances which have just been described, for he wraps up a fly and presents it to the female for her acceptance. If he is given a fly in the complete absence

FIG. 81.—Male Tarantula barbipes displaying legs before female. After Locket.

of a female, he eats it at once, without attempting to wrap it up, but if she is present, the fly is swathed in silk and held out for her to feel with her palpi. It is remarkable that the carnivorous male should be willing to refrain from eating his gift himself, and Locket has given his description a humorous touch by adding the record of a male which offered a fly it had itself previously sucked.

THE COURTSHIP OF CRAB-SPIDERS

There are the other families of spiders which hunt their prey, chief among which are the crab-spiders, or Thomisidae. These include several species in which the male

has a different pattern from the female or is to some extent decorative, and hence, though the sense of sight may not be very keen, we might expect to find acts of courtship in this family.

But this is not the case. When a male encounters a female, he climbs upon her back with no sort of preliminary. If she tries to escape he seizes one of her legs roughly in his jaws, to avoid so lamentable a loss. They may roll over and over together, but as soon as she ceases to struggle, he climbs upon her back again. The only sort of courtship is the tactile stimulation to which he subjects her, tickling her with his feet as he crawls about her back. In some species the male, before mating, ties the female to the ground with such a quantity of silk that she ultimately has some difficulty in tearing herself free.

Very few observations seem to have been made on the simple wandering spiders of the families Drassidae and Clubionidae. In some species the male finds the female resting in a silk cocoon. He taps upon it with his forelegs for some time, then tears it open and enters. Some males, such as that of the British species *Clubiona trivialis*, construct a mating nest next to the rest-cocoon in which the female is confined, and tap upon the partition between them, sometimes for days together. Other species have been seen to mate forcibly, the male seizing the female and showing her no consideration. In others, again, the male and the female tap each other with their front legs for a few minutes.

The courtship of the comparatively primitive spider, *Dysdera erythrina*, was described by Berland in 1912, but his account seems to have been overlooked by British workers. When the two animals came face to face, the male immediately placed his two forelegs over the female, with his claws on her abdomen, seeking to hold her still while with his second pair of legs he gently caressed her sides and the under surface of her abdomen. Both spiders had their jaws wide open, but as the male continued stroking the female, her aggressiveness vanished and she fell into a sort of hypnotic condition.

The Courtship of Web-Spiders—Agelenidae

The spiders which spin webs form a group somewhat apart from the active jumping species, since their sight is in general less keen and their sense of touch more delicate. The courtship of the spiders which spin the familiar tubular web is a very easy process to witness and has long been known.

If a male house-spider is put upon the web of a female, he at once begins a performance which is seen in no other circumstances. With his two palpi he vigorously drums upon the sheet of the web. The female, waiting in the tubular part of the web, is aroused. She feels the web shaking and behaves as if she was aware that this disturbance is not produced by any fly or blundering intruder. She waits expectantly and lets the vibrations play all round her. The male gradually approaches until he can touch her with his forelegs. The female of *Agelena labyrinthica* falls into a cataleptic trance as a result of this courtship. The male carries her about, by a leg grasped in his jaws, and she does not awake until mating is over.

A similar but more complicated courtship is exhibited by the spinners of the calamistrated bluish-looking webs, described in Chapter VII. Locket has given an account of it for the species *Dictyna latens* and *Amaurobius similis*, and Berland for *Filistata insidiatrix*. Berland's account is translated as follows : " There was established between the two animals a curious and complicated kind of telegraphy. The male advances on to the web and with his anterior claws, pulls strongly at the threads ; he taps impatiently, proceeds, retreats, circles round the female's retreat. One sees that he is delivering 'une veritable supplication amoureuse.' And the female replies, pulling the threads, in such a way that it is evident that a communication is established between the two, a real exchange of sentiments, but of a purely tactile nature. At last, after half an hour, the female decides to come out, and advances a little from her retreat. But she must be made to come out on to the

web, and the male goes to seek her. He caresses her with his front legs, he takes her by the hand, if I may use such an expression, which is, however, very exact. I have often seen him take up her fore-claws in his, and drag her gently towards him. Sometimes she is afraid, and escapes back to her retreat. Then he begins again."

The Courtship of Web-Spiders—Linyphiidae

This complex behaviour of *Filistata* is of great interest, for it more closely resembles the actions of the higher families of web-spinners than the lower ones. Nothing so elaborate seems to have been observed among the Linyphiidae—the spinners of the sheet-webs. For example, Bristowe thus describes the courtship of *Linyphia clathrata* : " He gently touched the web, first with his palps, then his legs ; these actions became more rapid, and very slowly he began to advance with quivering abdomen and palpi. Performing these motions he circled round the female, who remained motionless in the centre of the web. . . . Then a new set of motions were noticed. He stretched his front legs out in front of him and alternately bent them inwards, the tips of the legs remaining fixed to the web ; then, letting go with his front legs he began to rock up and down in the web, at first gently and then more rapidly ; finally, with some twitches of the abdomen and movements of the palpi he came to a standstill."

Other Linyphiidae which have been watched at courtship perform somewhat similar actions. It is important to realise, however, that many members of this family are the possessors of stridulating organs. These have been already described. They exist in the male only, usually between the chelicerae and the palpi, sometimes between lung-books and the fourth legs. It is particularly unfortunate that the courtship of such species seems not as yet to have been witnessed.

The character of the courtship is changing as we move about the scale of spider families. Dancing gave place to

tickling, and this has now been followed by shaking or drumming on the web. The hostility of the female has also been decreasing, and in the next group has not only disappeared, but is replaced by eagerness.

The Courtship of Web-Spiders—Theridiidae

The courtship of Theridiidae in some ways resembles that of the *Linyphia* described above—that is to say, the male plucks at the threads of the web. But there is often this difference, that the male's importunities coax the female out from her customary retreat to a place in the web which the male has prepared for mating. Locket writes thus of *Theridion pallens:* "A male on being introduced to a small case where a female had built her web, began crawling upwards, his abdomen pulsating slightly from time to time. Having found the female, who up to now had made no movement, he began walking about in her vicinity biting away threads and spinning new ones. He then hung inverted, his legs slightly flexed, and with the second pair began a series of rapid pluckings on the web, otherwise remaining quite still. The female, as though attracted by these movements, came slowly towards him, her front legs outstretched and waving. She stopped whenever the male stopped his movements (which were intermittent) and came on again when he recommenced. When she was quite close the male stopped."

The males of Theridiidae do not often live for long, and it may be because of the shortness of the breeding season that the females are generally less hostile than those of other families. In several descriptions of the mating of species of this family, emphasis has been laid on the ardent behaviour of the female, who sometimes takes the lead in the courting, and sometimes appears to be quite insatiable.

Again, in this family males are known which possess stridulating organs. The common brown British spider, *Steatoda bipunctata*, is the most familiar of these, but, though both Bristowe and Locket have described its court-

ship and mating, there is no reference to any movement which could bring the two halves of the organ into play. Bristowe, however, says elsewhere that he has seen such movements, without describing them. It would almost seem as if the possession of the organ were but an extra protection granted to the wandering males, who use it in the same way as do the trap-door spiders. This, however, is only speculation.

The Courtship of Orb-Spiders—Epeiridae

Finally we reach the head of the spider family, and come to the familiar species, whose pronounced ferocity to their mates has helped to give all spiders a reputation for cruelty.

Courtship in the common species, *Zilla x-notata*, is thus described by Locket: "The male climbs to the centre of the female's web, and usually seizes the line communicating with the female's hiding-place with his four front legs. With his back legs he seizes one of the adjacent radii at the centre, and starts a series of jerking and plucking movements on the communicating line, using himself as a sort of spring at the angle of the radii. If the female does not respond he then usually climbs to her retreat, but returns again after an interplay of legs. Eventually the female comes out, also making plucking movements."

An essentially similar procedure is described for the little green spider, *Epeira cucurbitina*, and the resemblance of that of the Theridiidae is obvious.

A sufficient number of instances of courtship have now been described to give a general impression of the proceeding, which must now be considered with the object of determining, if possible, its biological significance. It seems that the acts of courtship among spiders are more favourable for this purpose than those of any other sort of creature, for it is possible to compare the behaviour of the spiders which see with that of the spiders which feel (or "hear"). It becomes apparent not that some spiders

indulge in courtship, but that in all families the act of mating is preceded by various kinds of preliminaries, which appeal to the particular sense that is most highly developed.

Earlier Theories of Courtship

Three theories at least have been put forward in explanation of the courtship of animals.

Darwin saw in courtship an opportunity for a choice of a mate, an acceptance or refusal which, embodying a process of sexual selection, explained also the vivid colouring, ornamentation, or whatever secondary character the animals bore.

Wallace regarded such secondary sexual characters as recognition marks, which enabled the female to recognise the male of her own species. Thus their display tended to prevent the uneconomical act of an unfertile cross.

The third theory, due also to Wallace, regards the secondary character as a mere expression of, and the activities of courtship as a result of, the more vigorous metabolism of the male organism, without offering any further explanation of either.

These theories were put forward at a time in the history of Biology when Natural Selection was considered all but omnipotent. They make demands on the female's powers of discrimination which it is difficult to justify. Moreover, if they imply a direct connection between acts of courtship and secondary sexual differences, they ought also to deny the possibility of courtship where such marked differences do not exist. We have seen that this is not so. Again, secondary differences may exist, as in the spider *Micrommata virescens*, whose female is uniformly green, while the male has a vivid yellow and scarlet abdomen, without a corresponding utilisation in courtship. The third theory seems to imply that there is no necessary connection between the courtship of the male and the subsequent mating; that both courtship and decoration have a merely

bio-chemical origin and may be devoid of purpose or result. Further, as Peckham has shown, there is some reason for doubting whether the female spider is a less vigorous and active organism than the male.

It seems that the process of courtship is more intelligible if it is considered in its relation to the individuals concerned than if it is considered racially. For there is some certainty as to the physiology of the individual, but there is still a very considerable doubt as to the true way or ways in which the evolution of the race has taken place. This is the chief point in favour of Montgomery's and Berland's modified acceptance of Wallace's views. Montgomery interpreted the courtship as a mixture of the actions of excitement and self-defence; while Berland, who had seen male jumping-spiders courting nothing, that is to say, dancing when alone, attributed their activities entirely to physiological excitement.

The same concern with the individual rather than with the race, is a feature of the more recent theory of Bristowe and Locket. These authors interpret their observations thus. Since the male spider runs the risk of being killed and eaten by the female, the first use of his courtship antics is to enable her to recognise him as a male, and not to regard him as something to be eaten. When he has begun his courtship, the male spider is practically safe, but it takes a varying amount of continued solicitation to stimulate the female so effectively that she submits herself to him. Recognition and stimulation are therefore both necessary before mating can take place, and the essential characteristic of Bristowe's and Locket's hypothesis is that it for the first time includes a supposed necessity for preliminary "recognition," and so places a dual responsibility upon the actions of courtship. All these theories will be reconsidered later, when the behaviour of the two spiders themselves has been summarised and brought into perspective.

Behaviour of the Male

When the courtship of American jumping-spiders was the only known instance of these activities, it was natural enough to suppose that the sight of the female was the instigating cause of the male's dance. Berland, however, saw *Saitis barbipes* courting in the absence of a female, and Bristowe and Locket showed that the smell of the female would also stimulate male wolf-spiders to go through their courting actions. They describe the behaviour of *Trochosa picta* thus: "When a male of this species has come upon the trail of a female, he reminds one of a hound following up a scent. He becomes very excited, and appears to advance in a zigzag fashion along the trail, feeling the ground with his palps and the tips of his legs, often touching the ground two or three times with the latter before actually putting them down."

It was proved conclusively that sight was not used, for males of several species were seen to go through their performance when placed in a box which had previously contained a female. Water which had been shaken round her cage or particles of sand over which she had crawled or threads she had spun were found to be equally effective in exciting him to action, but threads dried and then baked would not do so.

However, this is not a specific reaction of the male spider to the scent of the mature female of his own species. It is possible to learn more by the study of a few abnormal cases than by much repetition of the ordinary, as psychotherapists know well, and many occasions of curious behaviour on the part of the male spider have been recorded.

Male spiders have been incited to begin their courtship actions before other males, both mature and immature, of their own species or even of another species. Peckham saw a male *Phidippus mccookii* court a female *Phidippus clarus*, while Locket saw a male *Tarentula barbipes* performing in front of a male *Trochosa ruricola*. These spiders, which were separated by a glass partition, were not

even of the same genus. Male spiders frequently court immature females, and Montgomery saw a male *Prosthesima atra* seize two young females at once. Again, Locket saw a *Tarentula barbipes* start his performance in a box which had previously contained a male, while males have been known to embrace the cast-off skin of a female, and to become excited on being placed in the empty web of a female or even of another male. It is clear, therefore, that the stimulus which initiates the male's performance is vague, rather than definite and specific. It may act upon the sense of sight, of smell, or of touch, but the appearance or the scent of the female does not seem to be readily distinguishable from that of the male.

Two curious actions are often exhibited by spiders during their courtship. One is a sharp twitching of the abdomen, which is sometimes violent enough to cause a distinct tapping sound as the ground is struck. This action, which was described by Campbell long ago, is probably due to extreme excitement or self-stimulation. The other is more difficult to understand. The spider stops its courting actions and rapidly rubs its legs together. On at least one occasion a female spider has also been seen to do this. It may be due to intense stimulation, or, since the legs contain sense organs, Bristowe suggests that it "may have the effect of sharpening the senses and be the equivalent to blowing one's nose or taking off one's gloves."

A final action which seems to mark the end of courtship in practically all spiders is a rapid thrust-and-parry or interplay of the forelegs of both sexes. The tactile spines are no doubt concerned here, so that whether the courtship was originated by sight or by scent, it is concluded by touch. As Montgomery says, "There is a language of touch," and doubtless all spiders can speak it well.

Behaviour of the Female

The part played by the female during the courtship of the male is usually much more passive, unless she happens

to be in no mood for wooing. It is very rarely that she actually kills a courting male; more often she chases him away. She may content herself with a particular menacing attitude; for instance, *Xysticus cristatus* " raised her front legs threateningly, giving a little jerk forwards every few seconds, whenever he approached. Although the male appeared to be quite ardent, he seemed to recognise this as a danger signal and retreated." Again, the female may gently but firmly push the male away with her front legs.

A male who is not performing the acts of courtship does indeed run a risk of being killed. Bristowe has recorded instances of this, including one of a *Pisaura mirabilis* who was killed because he had no fly to wrap up and present.

Some females, particularly those of the genus *Theridion*, respond almost immediately to the presence of the male. Locket tried the interesting experiment of putting males of *Theridion varians* into the webs of the very similar *Theridion denticulatum*. Some of the males were stimulated thereby, but the females invariably attacked them without the least hesitation, although they never attack males of their own species.

As courtship proceeds, the females become more stimulated. That this is so is not merely a hypothesis to explain the facts of courtship, but is borne out by evidence. The female *Leptyphantes leprosus* has a large downwardly-directed vulva and Locket has observed that this " was extended in a curious manner during the male's advances, while after mating it was found to be in its normal position again." The same thing was seen to a less marked extent in *Epeira cucurbitina*.

By this time the female is taking a more active share in the courtship. If she is a web-spider she may be giving jerks to the web, which help the male to locate her and which also stimulate him. Other spiders have been seen to reciprocate the leg-movements of the dancing male.

Relation between Male and Female

The popular notion that the female spider eats the male may now be considered more precisely. Such cannibalism is, as has been said, rare before mating and practically never occurs if the male is carrying out his courtship actions normally. The ordinary hunger of the one and the ordinary fear of the other are both swamped by the ardour of the sexual impulse—a fact which is true of many other animals besides spiders. As will be noticed later, male and female spiders of several different species may often be found living in the same retreat.

As opposed to monogamy, polygamy and polyandry may readily occur if the male escapes successfully. He may then mate with any other female he may meet, just as he may mate with the same female again and again, and just as the female may mate with other males who discover her. Locket has seen males of *Lycosa pullata* mating with females which were already the owners of egg-cocoons ; but an even better example, observed by Abraham in Taiping, was recorded by Hogg. A web of the large orb-spider, *Nephilia maculata*, contained a female and three males, all three of which were seen to mate with her in a short interval of time.

The Significance of Spider Courtship

What is the real significance of spider courtship, considered as a whole ? It must be realised at the outset that even yet the observations which have been made are not sufficiently numerous to yield conclusions which are more than tentative. No certainty, no dogmatism is possible in the existing state of our knowledge. The theories which have been put forward by previous workers have already been mentioned, and the objections to some of them have been stated.

The latest theory, that of Bristowe and Locket, seems to err in being needlessly complex and in attributing mental

powers to the spider which it probably does not possess. The idea that the female must first recognise the male so as to distinguish him from edible prey is superficially attractive, but it is open to two very serious objections. In the first place, " recognition " is a psychological term which presupposes a state of awareness or consciousness in the spider, and it therefore offends against the canon, stated in the chapter on behaviour, that all actions should be interpreted in their lowest possible terms, rather than in their highest. It will be shown later that a simpler interpretation is possible in the instance of courtship.

In the second place, " recognition " is clearly not the right word to use, since a virgin female cannot recognise that of which she has had no previous experience. " Realisation " might better express the female's seeming ability to distinguish mate from prey, but even so, it is too strong a term.

Such realisation as does exist occurs first when the male sees, smells, or feels the female, and so begins his courtship, whether it be dancing, semaphoring, or plucking the web, and whether she is actually there or not. The " recognition " theory seems to imply that the male is better able to recognise the female than she is to recognise him. Otherwise he would run away. The theory neglects the fact that the male has to suppress his natural fear of a bigger spider just as much as the female has to suppress her normal instinct to feed. It cannot be supposed that the male can see or smell the female before the female can see or smell the male, for the fact that a spider would begin its courtship in a box which had previously contained a male, shows that males, no less than females, can be smelt by other spiders.

Even if we grant that this realisation is a part of the courtship, we must assume that it results from the effect of courtship upon the female. Courtship produces physiological changes in the female, which begin by resulting in " recognition " and ultimately result in stimulation. Where does the distinction commence ? It is clear that, looked at

from the point of view of female physiology, the two processes are inseparable. All courtship, of whatever character, is nothing more than an appeal to the "mind" of the female, and nothing is gained by dividing that appeal into indistinguishable stages. Looked at critically, the "recognition plus stimulation" theory fails to establish its claim.

It fails to do so because it demands too high a degree of mental development in the participants. If the actions involved in courtship be compared to those described in the chapter on behaviour, it is seen at once to what category they belong. They are instinctive actions of the chain-instinct type, and it is as such that they may best be interpreted.

The origin of the whole business is the maturation of the testes of the male spider. When his final moult has been accomplished, the whole character of his actions changes. He ceases to spin a web and becomes a wanderer. It is possible that a hormone, such as is known to exist in vertebrate animals, is responsible for his changed attitude towards life, and that the male rapidly reaches a condition in which the sight or the scent of another similar spider, not necessarily the mature female of his own species, is sufficient to initiate the first of his series of instinctive actions. He begins his courtship.

It has already been pointed out that actions of the chain-instinct type require some definite stimulus to set them in motion. One is reminded of Ogilvie's observation that young partridges reared under a hen never squat when danger threatens, as the young birds always do in natural conditions when they hear the parental signal. "The necessary stimulus is absent, and that stimulus is supplied by one particular cry of the parents and nothing else."

After courtship has proceeded for some time, there always comes an occasion of contact between the two spiders. The common "interplay of legs" has already been mentioned: in some spiders it is a slower touching of the forelegs, or an actual "shaking of the hand," claw to claw,

as in *Filistata*, or a meeting of some other part, as in the case of *Pachygnatha listeri*, where the male seizes the chelicerae of the female with his own. Whatever it may be, the moment of actual contact always occurs. I interpret this partly as a test of conspecificity: males which have been courting empty boxes or their own mirror-image or another male or an immature female proceed no further with their activities when this test cannot be made or when it reveals the wrong spider. When, however, a positive answer is made to this tentative, further results follow.

It has often been noticed that the male himself becomes more stimulated as courtship proceeds. This may be due to the continued presence of the female, or to the repeated contact with the threads of her web or with her legs. It is clear, however, that the final touching of the female leads to the next and last link in the chain, when the male climbs upon the female's back or otherwise takes up the correct position for copulation. The male is now sufficiently stimulated to be able to exert the very considerable effort which is necessary to the ejaculation of the spermatozoa.

The "appeal to the mind of the female" produces results which are generally less conspicuous but not less important. The first effects of the male's presence must be an inhibition of the female's desire to feed. It is clear that an internally produced hormone cannot do this, or otherwise female spiders would have to fast. Hence the female refrains from attacking the courting male. During the whole of the courtship she is receiving impressions by the eyes, or the scent organs or the organs of touch. It is reasonable to conclude that when the central nervous system of the female spider receives notice of the courtship, from one sense organ or another, it reacts to the impulse and directs activities in other parts of the body. Actual change in the position of the vulva has already been mentioned, and there may be other changes which, being internal, are not manifest from without, but may none the less be essential if the mating is to be successfully consummated. Only the central nervous system can induce such changes,

and only when stimulated by the receipt of the appropriate intimation of so great a change in the environment as the arrival of a mate.

If we may venture to summarise in a few words the results of so complex an activity as courtship, we may say that courtship is a chain of related instinctive actions, in which the reproductive urge suppresses the normal habits of self-protection and self-nourishment, and is accompanied internally by the physiological changes necessary to make the subsequent union possible.

CHAPTER XI

THE MATING AND PARENTHOOD OF SPIDERS

THE duties of parenthood are very unequally divided among spiders, for they fall entirely upon the mother. Although some male spiders continue to live in company with the female after mating, there seems to be no instance on record of a male spider performing any act likely to benefit the coming generation. As he lives on the female's web he is little more than a dependant, taking his share of the captures and doing nothing in return.

Sperm Induction

There is, however, one important act which the male spider must perform in preparation for fatherhood, and that is the charging of his palpi with sperm. It has already been stated that the spider is one of the few animals in which the intromittent organ is separated from the testes, and the consequence of this separation is seen in the act we are about to describe.

The process was first observed and explained by Menge in 1843, but very few other zoologists during the nineteenth century offered confirmatory accounts. Some failed to witness it at all and concluded that it could not be of general occurrence. But the number of descriptions is now sufficient to give us a good idea of the nature of the act, which is certainly not one that can be very readily observed.

There seems to be considerable constancy among the different families in their carrying out of this process. The male spider spins a small sheet-web of very fine silk, some-

times upon the ground, sometimes among the branches of the plant upon which it is living. For many species the making of this web is the only spinning activity exhibited by the mature male. The length of this sperm-web is about half the length of the spider itself. The spider, standing over the sheet, deposits a minute drop of seminal fluid upon it, a drop so small that it is not easily seen. The palpi are then applied to the drop, alternately and repeatedly. Often they are applied to its under side and the fluid is absorbed through the web: sometimes one palpus is slowly waved in the air while the other one is being applied to the drop.

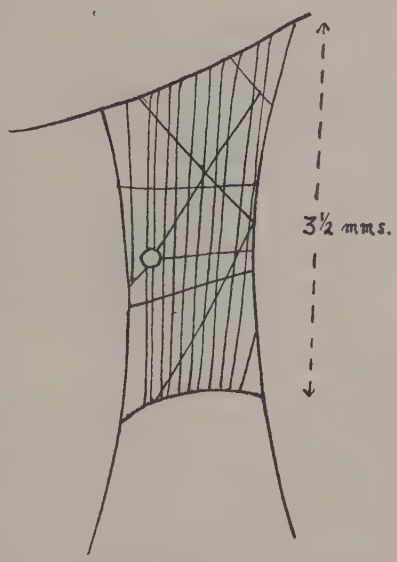


FIG. 82.—Sperm-web of Xysticus cristatus. After Bristowe.

Some spiders, like *Xysticus cristatus*, whose sperm-web is shown in Fig. 82, place the drop on the lower surface of the web and apply the palpi to the upper surface. Others again do not employ a web at all. They may use a few threads instead, as does *Linyphia clathrata* (Fig. 83), while Hull has seen *Linyphia montana* deposit the droplet on a leaf of

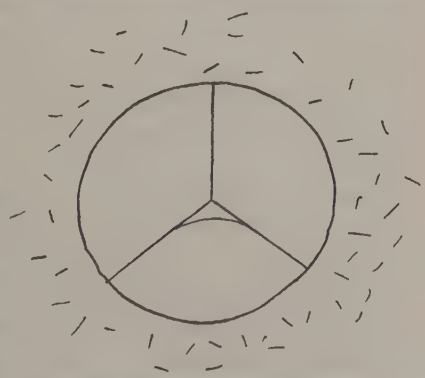


FIG. 83.—Sperm-web of Linyphia clathrata. After Locket.

the bush and *Lycosa amentata* on a dead leaf on the ground.

In these examples, mentioned by Hull, courtship and mating immediately followed the transference of the sperm to the palpi, and it would seem that sometimes the process is withheld until the female has been found. On the other hand, most of the occasions witnessed by Montgomery immediately followed the mating. Locket has recorded the most interesting case, in which a male of *Theridion sisyphium* recharged his palpi with sperm after each application to the female, approaching and retiring from her and then approaching again several times within an hour and a half.

Copulation

The relative positions taken up by spiders when in copula are diverse, but within the limits of each genus seem to be almost constant. There is also a degree of constancy within the limits of each family. Individual eccentricities, however, are found.

The position is dependent on the relative sizes of the sexes and on whether the meeting occurs on the ground or on a web. In the former instance, the male most usually mounts upon the back of the female, his head pointing in the opposite direction from hers. The female generally maintains a normal position, but may be partially pulled over to one side or even bound down with silk. Occasionally the smaller male is compelled to creep underneath the female's abdomen before he can reach the epigyne, and then their heads are, of course, pointing in the same direction. Alternatively, the male and female may be merely facing each other, their bodies in one line, or the male may creep right under the female and turn over so that their ventral surfaces are next to one another.

When the spiders meet in a web, the position is usually one in which the ventral surfaces are opposed to one another. They may be facing in the same or in exactly

opposite directions and may or may not be in close contact or embrace.

Whatever the position may be, it seems to be constant for every species, and this is no doubt due to the fact that the male palp is, as has been mentioned, a very complicated organ. It is possible that in one and only in one position is it capable of being inserted at all. This implies the impossibility of cross-breeding between two different species, and it is noteworthy that, while male spiders have several times been seen courting the females of other species, no single instance of an actual copulation between different species has been recorded.

All the possible variations in the mode of palpal insertion have been observed. In some instances the two palpi are inserted simultaneously. There is a group of families of spiders, designated Haplogynae by Simon, characterised by having a symmetrical epigyne divided into two similar halves, and in these families this method of insertion seems to be the usual one. It occurs, however, in exceptional species of other families.

In other cases one palpus and only one is used. Generally the palpi are used alternately. Each may be used once in this way, or several insertions of one palp may be followed by several insertions of the other. The total number of insertions during one mating varies from one to over a hundred. There is no doubt that this detail is influenced to some degree by the condition of the spider, and probably also by such physical conditions as temperature. Furthermore, the time taken in mating varies from but a single second to several hours.

The behaviour of the female during mating is also variable. She may be bound up tightly, and generally she is completely passive, falling in some instances into a trance-like cataleptic state. On the other hand, the females of some species seem to be quite undisturbed by the process and may be seen running about in the ordinary way with the males clasping their abdomens.

The male's activities during mating are more complex.

He has often to raise the abdomen of the female and may experience considerable difficulty in so doing, so that he must try and try again before succeeding. He may find insertion of the palp difficult, particularly if he has only recently moulted. In an extremely interesting observation of Bristowe's, a male *Micrommata virescens*, less than a week past his final moult, was found to be unable to copulate successfully until after an hour's fruitless efforts. This species bears a small spur or apophysis on the penultimate joint of the palpus, and this spur has to fit into a special groove in the epigyne (Fig. 84). In this case the pressure

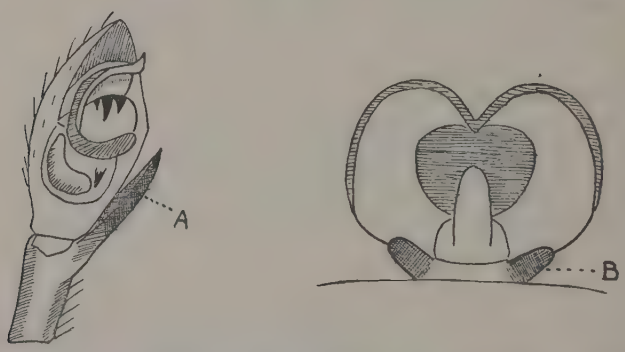


FIG. 84.—Male Palp and Female Epigyne of Micrommata virescens. A, Tibial apophysis. B, Groove into which apophysis fits.

exerted by the swelling of the haematodocha forced the rather soft spur out of place.

The male often pauses during the mating to pass his palpi through his jaws. Blackwell recorded this in 1873. Locket has watched the process through a microscope and has seen that it is actually the style of the palpal organ which is being passed through the chelicerae. It is probable that the style thus receives a necessary lubrication from the fluids of the mouth or of the maxillary glands.

Another very interesting observation of Locket's is concerned with the time occupied by the insertion of the palpi of the little spider *Theridion varians*. The first application of each palp lasted about a minute, but there-

after (each palp being applied forty-five times) the time taken dropped to six or seven and later to three seconds. Locket's conclusion is, " It seems probable that only the first two or three long applications of the palp are really effective and that innumerable short subsequent applications are not really functional at all, but only take place because they are pleasurable to the male, who in the intervals between the applications keeps the female stimulated by his taps on her sternum." To bring this conclusion of the pleasure-loving, self-indulgent male into line with the view we have taken of the instinctive nature of all these actions would require a discussion—obviously irrelevant here—of what is implied by the word " pleasure," both for man and for the lower organisms. It is possible to supplement Locket's conclusion by the suggestion that there is a similar " pleasure " felt by the females of some species, who, apparently insatiable, continue to signal to the males by the jerks on the web long after the males have ceased to respond.

The Cannibal Female

The widespread belief, promulgated from book to book, that the female spider devours the male after mating, is very far from being justified by the facts. Perhaps the too facile acceptance of the generalisation may be condoned in some measure since the garden-spider, *Epeira diademata*, the best known of all British spiders, and one which to many represents the whole order, is a particularly fierce species and undeniably addicted to cannibal practices.

It is a fact that the females of several different species have been seen to kill and eat the males after mating. Much more rarely it happens that the murder is committed before mating. A male spider in the neighbourhood of a female is stimulated to begin his acts of courtship, and it seems that when he is performing these he is comparatively immune from attack. It has already been suggested that his courtship stimulates the female's reproductive instincts so that for a time they dominate her

pugnacious habits. When mating has been accomplished, a very different state of affairs obtains. The sexual impulse has died down and normal reactions return. It is now that the male is in the greatest danger, and not infrequently he makes off at his best speed. A certain proportion, however, undoubtedly perish at this time, especially, as Bristowe points out, towards the end of the mating season, when the vigour of the males is decreasing and their power to escape rapidly is consequently lessening. Locket thus describes the behaviour of a mated *Phyllonethis lineata*: "The female now suddenly started to attack the male by throwing viscid lines on to him, and he was removed. He had already mated with another female who had treated him in exactly the same way, and he would certainly have perished had I not removed him." A "pregnant" female will often attack a male, almost at sight: his courtship makes no appeal to her.

The relative security of the male before mating is against Montgomery's theory that the male's courtship activities are but an exaggeration of the usual expression of fear, and so is the fact that many of the courting actions are quite unlike those exhibited on any other occasion. The post-nuptial risk admits of the possibility of competition between males, which would result in a kind of sexual selection, for those males that escaped would have a chance of mating again with other females. It is therefore probably true that the males whose appearance or whose courting actions are the most pronounced are the most likely to leave descendants, because, as Montgomery has said and Bristowe, following him, has emphasised, they "most quickly and surely announce themselves to be males." Thus they secure the pre-marital immunity, but the theory does not take account of the second danger period, after mating.

The males that run the greatest risks are those of the species whose mating period is prolonged. When males are likely to arrive at any time between September and April, as is the case with *Amaurobius ferox*, for example, the females are not so ready to "love, cherish, and to obey."

A meal may be preferable, and there is also a greater chance that the female is already " pregnant." It must be remembered that her actions are governed more by her internal physiological condition than by her " state of mind."

In other cases, when the mature male has only a transient existence, the females are seldom hostile and often eager. In such instances the risk to the male before mating is negligible, and it is much less afterwards, although accidents may happen at any time. Quite often it happens that male and female live together in the web, not only before mating but even afterwards, and sometimes for a considerable period. Males of *Linyphia triangularis* are generally found in August in the female's web, and I have found both *Epeira quadrata* and *Epeira cornuta* living in pairs in the same nest. I have known a pair of *Pholcus phalangioides* to continue to share the same web until after the hatching and dispersal of the family ; but this is probably exceptional. In a few extreme cases the partners are sufficiently tolerant of one another to share their food, as Locket has described for *Dictyna uncinata* and we for *Agelena*. It is, however, always probable that such partnerships depend for their continuance on a sufficient supply of insect food, when the predatoriness of the spider tends to be subdued.

Egg-laying and Cocoon-making

The mother's share of the duties of parenthood begins when she lays the eggs and spins the cocoon round them. The eggs are never laid singly, but it is said that the cocoon of the common species *Oonops pulcher* contains only two. Most spiders make only a single cocoon, but there are many that spin two or more. Probably the actual number of cocoons made in such cases is more dependent on the conditions of life, and the fortunes of the spider than on the spider's specific identity. For example, the house-spider, *Tegenaria atrica*, usually makes three cocoons, but well-fed captive species have been known to make twelve.

The cocoon is much more than a mere egg-bag. It usually includes some protection for the eggs within, and in not a few cases its finished appearance is as characteristic of the species as is the form of the spider itself. Generally, however, it is spherical or lenticular in shape.

The process of laying the eggs and spinning the cocoon around them is not nearly so difficult to observe as the process of sperm-induction, partly because female spiders are easier to keep in captivity than males, partly because it takes much longer to accomplish, and partly because its approach is indicated beforehand by the actions of the mother. It has the disadvantage that it usually takes place in the evening and may keep the watcher from his bed until the small hours.

If one may judge from the numerous published descriptions, there seems to be considerable similarity in all the processes of cocoon-making and it may be more useful to give a general outline of the process, rather than descriptions of what occurs in a few selected species. Nearly all the original descriptions are in readily accessible papers.

The first stage is generally the spinning of a small sheet of closely woven silk, upon which the eggs are to be laid. Sometimes, however, as in the case of *Agelena labyrinthica*, the egg-cocoon is contained in a silk chamber of its own, and then the making of this chamber is the first care. It may occupy the whole of the previous day and only shortly before midnight is the little sheet placed inside it. The size of this sheet roughly corresponds to the length of the spider's body.

In the simple cocoons, the eggs are now laid directly upon this sheet, but in a great many species, a flocculent layer of downy silk intervenes between the sheet and the eggs. This beautifully soft material is jerked out of the spinnerets, which are themselves working like scissor-blades during its production, and it is to these movements that the downy consistency of the substance is due. It has been mentioned already that this protective layer is the product

of a special set of silk-glands, and that it is often yellow or brown in colour.

The eggs are laid upon this cushion. It is only rarely that they are laid so as to be separately visible. Generally a drop of fluid is exuded from the mouth of the spider's oviduct, comes in contact with the sheet, and then increases greatly in size. The drop remains, however, connecting the sheet with the oviduct, and the eggs pass gradually into it. This fluid is probably in part a lubricant, but it seems also to have another function.

It is slightly alkaline, syrupy in consistency, and suspended in it are numerous small round particles. When it evaporates, these particles are deposited on the surfaces of the eggs, giving them a bloom like that on grapes. This layer prevents the eggs from sticking together into a solid mass, as they would otherwise do, with fatal consequences. It also strengthens the outer covering of the egg, which, instead of being very delicate, becomes firm and elastic.

The eggs of hunting-spiders, which have spun the first sheet near the ground, are laid downwards upon the upper surface. Web-spinners, working at higher levels on the vegetation, generally lay their eggs upwards upon the lower surface of the sheet. In many individual cases, such as that of *Palystes* described by Warren, it is far from obvious why the eggs do not at once fall from their correct position.

The eggs are then covered with the intervening padding, when this is used ; and lastly, another sheet is spun over all. The lower sheet is then generally freed from the ground so that the whole cocoon may be picked up and finished by turning it round and round by the legs while the spinnerets cover it with more threads of silk. This rounds it off and seals up the equatorial joint.

In many cases the cocoon is now finished. It may be retained in the mother's possession, or fastened to a stone, or to a fence, or it may be suspended on a stalk, as in the examples shown in Fig. 85. Again, it may be covered with a protecting coat of mud or of small pieces of wood or of

tiny stones, which make it less conspicuous and also help to render it immune from the attacks of Ichneumons.

The size of the spider's abdomen is always much reduced by the laying of the eggs. In some spiders the reduction is so marked that the abdomen is conspicuously wrinkled even before the actual laying is completed.

The Cocooning Instinct

Mistakes are sometimes made in the placing of the eggs, and these mistakes are never corrected. The empty cocoon is carefully finished, while the eggs remain exposed beside it or lie on the ground below. This illustrates the nature of the actions which the spider performs in cocoon-making; they form yet another series of instinctive acts of the chain-instinct type. Virgin spiders generally follow the same course as do those that have been fertilised, and construct with equal care cocoons of infertile eggs. Several spiders have been known to devour their infertile eggs as soon as they were laid, but it is not certain whether this is due to the unnatural circumstances of captivity and to some disturbance occasioned by the observer, or whether the spider "knew" that the eggs could not hatch. However, the fact that virgin spiders behave like this shows that the series of instinctive actions is initiated by the maturation of the eggs within. Probably external sensations of touch decide the choice of the actual spot where the cocoon is made: for example, Montgomery noticed that a large proportion of his captives began the first sheet on or near a drop of water which was lying in the cage.

It would be difficult to find a more beautiful instance of the complementary nature of the male and female characters, than this comparison between the sexes of spiders. Maturity in the male impels it to give up web-spinning, to take to a wandering life and to commence courtship when a suitable opportunity occurs, while maturity in the female impels it in due course to perform

in the correct order all the complex actions necessary for making a cocoon.

Forms of Cocoon

It is not surprising that, since it is possible to trace an evolutionary series of web-forms, something of the same kind can be done for cocoons. It is not quite so satisfactory a succession, because there is only a general and not a complete resemblance between the cocoons of all the species of any one family, while some of the most striking

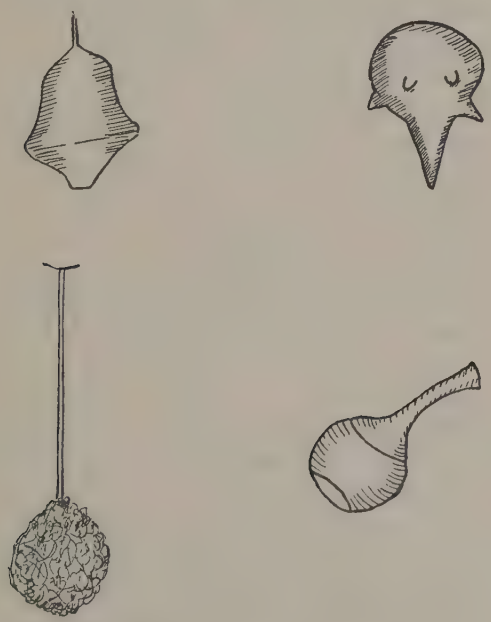


Fig. 85.—Spiders' Cocoons.

and complex forms of cocoons appear at comparatively low levels.

It seems fair to assume that if the primitive nest was no more than the lining to a cranny, the primitive spiders merely laid their eggs against the side of the nest. The first step in the production of a cocoon came when the egg-

mass was provided with a protective cover. This condition probably remains with the Liphistiomorphae and some of the simpler Mygalomorphae. The next stage is the provision of a special base on which to lay the eggs, which are then covered simply, as before. This condition is general among the wandering Drassidae and Clubionidae and the jumping Salticidae, spiders which only spin chambers for mating, moulting, egg-laying, and wintering.

Among the Clubionidae, however, some of the most wonderful of the cocoons are found. The best-known examples are those of the common British species of the genus *Agroeca*, whose cocoons resemble miniature wine-glasses, coated with a thin layer of mud (Fig. 85).

In the next stage the cocoon, consisting still of base and cover, is spun away from any nest. These are represented by the lenticular cocoons which the wolf-spiders carry about with them, as well as by the small flat cocoons, fixed to stones and the bark of trees, which are produced by many of the smaller Linyphiidae.

In the last stage the cocoon differs from those just mentioned only in the addition of a middle layer of soft down, or an outside wrapping of protective substance. These are the cocoons of the Theridiidae and Epeiridae. Some of these may be suspended on stalks, like those of *Theridion varians* or *Meta menardii*, but the majority are plain spheres or hemispheres, either hung in the web or attached to some solid surface.

The outer layer of protecting substances may be composed of anything which lies accidentally at hand, as in the case of ordinary house-spiders, or of material actually determined and sought for, as in the case of *Agroeca*.

Care of the Cocoon

Many spiders, perhaps the majority, pay no heed to their cocoons after they are finished, and die sooner or later after the labour of completing them. This is true of practically all the Linyphiidae and most of the Epeiridae,

the exceptions among the latter family being those which so closely resemble their own cocoons that they acquire a degree of protection by continuing to live among them. It is also true of many of the simple wandering spiders, but some of those who spin a silk chamber all round themselves and make their cocoon inside it do not forsake their eggs, remaining in the nursery on guard for some time.

Among wolf-spiders, and Theridiidae and several others, however, personal concern for the cocoon is the general rule. The possession of a cocoon changes the mother's entire outlook on life, and her regular reactions to certain stimuli are very different after the eggs have been laid.

Most of the Theridiidae hang up their cocoons near the little bell-like retreat in which they themselves rest, but one common British species, the small brown *Theridion bimaculatum*, always clasps hers in her legs and carries it about. These spiders vigorously attack anything which ventures to approach or threaten their cocoons, but there are exceptions to this. Montgomery has recorded that *Theridion tepidariorum* often hangs up enshrouded flies close to her cocoon. When she has finished feeding, she cuts the fly loose and lets it fall; sometimes the cocoons fall with it, and in such circumstances the cocoon is not raised into the web again.

Crab-spiders generally mount guard over their cocoons with some tenacity. Montgomery observed that *Xysticus stomachosus* after completing her cocoon would not leave it for ten days, even to secure food. After ten days she would leave it to chase prey, but always returned to her charge. Bristowe described *Diaea dorsata* as sitting on her egg-cocoon, catching such small insects as came her way. She bit fiercely at larger ones to drive them away, stretching out her front legs and jerking her body in a way which seems to be a recognised sign of hostility. Similarly *Ctenus malvernensis* when threatened falls on her back, spreading wide her legs and opening her chelicerae. *Palystes natalius*, the African Sparassid, is equally determined. The female will not feed while she is guarding the

cocoon, though sometimes she will take a little water. If an insect approaches, she seizes it with her chelicerae and throws it down with very manifest purpose. As a rule, when she is not hungry and has no cocoon, she simply moves away from any insect that may touch her, without attempting to bite it. A member of another family, *Drassus neglectus*, carries her cocoon about with her, and refuses to feed while so occupied.

But care of the cocoon, as distinct from care of the newly-hatched young, reaches its climax in the families of Pholcidae, Pisauridae, and Lycosidae.

It is well known that *Pholcus phalangioides*, a common species in the south of England, carries her cocoon in her chelicerae. The cocoon in this instance is so flimsy that the eggs are easily visible—indeed it is only after the young have hatched that one can see, from the thin silk case that is left, that a real cocoon has been surrounding them at all. Generally the mother retains her hold upon the cocoon until the eggs hatch, but occasionally she has been seen to hang it up while she cleans herself or feeds. With some difficulty, even with the help of her second and third legs, she frees her jaws from the cocoon, touches it with her spinnerets, and suspends it from a few threads of the web. When she has finished she returns and takes up the cocoon again.

The Pisauridae, a family of hunters related to the wolf-spiders, include a species, *Pisaura mirabilis*, which is very common in England. The cocoon is a large cream-coloured sphere, which the mother carries about under her sternum. When the young spiders are nearly ready to emerge, she fixes it to the end of a branch of a shrub, and all round and about it spins a beautiful silk nursery. Outside this she mounts guard for the rest of her life.

Female Lycosidae carry their cocoon, as is well known, attached to their spinnerets, and guard it with great tenacity. If it is forcibly taken away, the spider seems at first to be stupefied, she moves slowly, as though dazed, with none of the rapid precision which usually characterises her movements.

It is evident that her organisation at this time of her life demands that there be something in contact with her spinnerets. If the cocoon is taken away and she is presented with it again, so that she can feel it, for she is unable to recognise it by sight, she immediately fastens it to her spinnerets and regains all her former activity. Peckham showed that the spider generally retains her response to the restored cocoon for sixteen or seventeen hours, seldom as long as twenty-four hours, and in no case for forty-eight. It is tempting to ascribe this apparent desire of the spider for her cocoon to maternal affection, but in reality her actions are nearer being automatic. She does not discriminate between her own cocoon and that of another species, and accepts with equal readiness a pith ball or a pellet of cotton wool. Locket has recorded an instance of a *Lycosa palustris* found running about in natural circumstances with a small snail-shell attached to her spinnerets. Evidently the spider is impelled from within to carry something, and it is not essential that this something shall be her own cocoon.

In this respect wolf-spiders are in interesting contrast to the African *Palystes natalius*. These females, when offered their own cocoon and that of another spider, have no hesitation in choosing their own. They decline to attend to another cocoon if their own is available, and if the two cocoons are put into the cage and the spider is placed on the wrong one she will desert it and go to her own. It is probably by smell that the spider detects her own cocoon, but sight may also help. On one occasion a spider deserted her own badly misshapen cocoon in favour of another properly made one ; and again another's cocoon was preferred to her own by a spider whose cocoon was stained with aniline dye.

Spiders of the family Theridiidae, which live in close association with their cocoons, will also refuse substitutes. In no case, however, would true associative memory seem to be involved. The spider's actions are instinctive responses to a particular stimulus.

Hatching: Care of the Young

As a general rule the young spiders escape from the cocoon without any help. They may be able to bite through the imprisoning threads, but it probably more frequently occurs that the cocoon simply splits at its weakest part, when the pressure of the youngsters within becomes great enough. Many cocoons, as has been stated, are made of a base and a cover, and the equatorial seam where these meet is more readily torn. Fabre has described the almost explosive rupture of the cocoon of *Epeira fasciata* when brought into the warmth of the sunshine. Several of the spiders which live close to their cocoons and guard them from intruders, take some share in the emergence of the young. It seems to be the general rule that such Theridiidae, Pholcidae, and Thomisidae cut open the cocoon when the moment has arrived; and Fabre, in a sentimental mood, describes this action as the last act in the life of the crab-spider, *Thomisus onustus*.

Generally, however, the mother survives and a sort of family life may follow. Co-operation of this kind is rare among spiders, and its occasional occurrence is therefore interesting. It emphasises the wide diversity of habits in the order.

Wolf-spiders give their newly-hatched young more attention than do most other spiders. As soon as the spiderling has scrambled from the cocoon, it climbs upon its mother's back, where with its numerous brothers, it maintains a precarious foothold until it is strong enough to fend for itself. The mother presents a very curious appearance with the crowd of young ones all over her abdomen and part of her cephalothorax. It has been said that the young refrain from crowding upon the mother's eye-region, but the truth is that, if any should venture too far forward, the mother gently but firmly sweeps them off with her leg. They are often scattered by accidents, but do not voluntarily descend, except when the mother is drinking, when a few have been seen to scramble down to

the water's surface and back again after assuaging their thirst.

The habits of the mother-spider do not seem to be so strongly influenced by the possession of the hatched brood as they previously were by the presence of the cocoon. The loss of half her family does not seem to be regarded as a catastrophe, and conversely the mother-spider raises no objection to taking on the additional burden of another spider's offspring, should any happen to come aboard. Warburton gives an account of a fight between two mother wolf-spiders, after which the scattered broods climbed upon the victor as she ate her victim, and Fabre says that three families may be accommodated on the same spider.

No other kind of spider carries her young about with her so solicitously as the wolf-spider. The nearest approach is among the Pholcidae, whose young immediately after hatching cling to the chelicerae of their mother. They do not as a rule stop very long in this position.

The brood of some web-spiders continue to live for a short time in the protection of the parent-web. Young trap-door spiders are in no immediate hurry to leave their burrow. The most striking developments of a family life have been described by Locket among some of the Theridiidae, particularly *Theridion sisyphium*. The mother and all her offspring live in the same web. When a fly is entangled the mother attacks and kills it; she then bites its body in several places. The young ones make their way to the fly and, crawling over it, feel it with their palpi. They stop at the soft spots, particularly at the holes made by the mother, and rhythmical movements of their body then follow, showing that they are sucking vigorously. Locket's most striking discovery is thus described in his own words: "On several occasions I found two or three young spiders collected round the mother when she was not feeding, and on examining them with a microscope found that their mouths were applied to hers. Presumably, then, she was feeding them. I have never heard of another instance of this habit among spiders."

Fertility

The fertility of spiders varies very greatly. It is least among the species that care for their young or are well protected, by coloration or by specialised habits, from their natural enemies. It is greatest among those that leave their cocoons to chance and that lead lives exposed to the attacks of wasps and ichneumons.

We may take *Dictyna uncinata* as an example of the small family type ; it produces something under thirty-five eggs a year, but some rarer species have far fewer. Thus *Oonops pulcher* makes several cocoons each containing but two eggs ; *Synageles picata* lays three eggs.

The large British spiders, *Epeira quadrata* and *Epeira diademata*, lay about six hundred eggs, and the wolf-spiders have about the same number. The African *Palystes natalius* reaches about eight hundred. The cocoons of the large American Epeirids contain from fifteen hundred to more than two thousand eggs, while some of the large trap-door spiders lay as many as three thousand eggs.

When the population of spiders remains approximately constant in numbers there must be a relation between the fertility of the species and the risks to which it is exposed, so that of the progeny of a pair of spiders, a pair survives. At present our knowledge of the details of the life of spiders is inadequate to explain the great differences in fertility that are known to exist.

CHAPTER XII

THE DEVELOPMENT OF SPIDERS

BIOLOGICAL theory looks upon the animal or plant as an assemblage of a vast number of units known as cells. Each cell is, to a certain limited extent, an independent unit, bounded by its own cell wall (when one is present) and controlled by its own nucleus. Each cell has originated from the division of some pre-existing cell and can, by division, itself produce more cells. Thus the whole of an animal's body has in the course of its development and growth arisen from a single cell. Indeed, the whole animal and plant population may be regarded as the outcome of an enormous number of generations of cells, stretching back into remote antiquity to their origin in the first speck of primordial living matter.

CELL-DIVISION

The individual animal normally comes into being when the egg-cell or ovum of the female parent is " fertilised " by the spermatozoon of the male. The product is a zygote, a single cell capable of a development which neither of its producing gametes can bring about alone. This chapter is concerned with the origins of the gametes in the gonads of the parents, their fusion and the subsequent development of the zygote. It is necessary first to understand something of the process by which cells divide, the process called mitosis or karyokinesis.

The nucleus, in which the control of the cell's activities is evidently vested, consists of a special protoplasm called

nucleoplasm, in which lies a mesh of darkly-staining threads, the chromatin network. The whole is surrounded by a nuclear membrane, outside which lies the centrosphere, a star-like body, whose nature is something of a mystery.

In the process of cell-division, the nuclear membrane disappears, putting the nucleoplasm into continuity with the cytoplasm of the rest of the cell, and the chromatin network is rearranged, forming a continuous thread or skein. This skein breaks into a definite number of short pieces, the chromosomes. Meanwhile, the centrosphere has divided and the two halves have moved apart, still, however, connected with one another by a number of very delicate rays. To the equator of these rays the chromosomes become attached and lie in one plane across the middle of a spindle-like figure. The chromosomes are split longitudinally and the split half-chromosomes are borne on the ends of the rays of the now separated centrospheres. Skeins are now reformed, chromatin networks and nuclear membranes follow, and the segregation of the protoplasm round the two daughter nuclei completes the formation of two cells from the original one.

In this process of typical mitosis it is to be noticed that the cytoplasm of the cell plays no part. Further, the number of chromosomes produced is a fixed and definite one for each species, and is known as the species number. In man the species number is 48, in many spiders it is 14, in others 24 or 54. The chromosomes are split longitudinally and not transversely, which means that if a chromosome be (as it probably is) a linear aggregate of smaller units not necessarily all alike, the two daughter chromosomes resemble each other exactly. They would not do so if the division were transverse. According to most cytologists all the inheritable characteristics are represented somehow in the chromosome; hence the interest which attaches to these bodies arises from the fact that in studying them we are studying, as nearly as is yet possible, the actual carriers of inherited traits. Chromosomes will be referred to again in this chapter.

Oogenesis

In spiders the first signs of the developing ovary appear in the embryo some days after the egg has been laid, as two narrow longitudinal strands of tissue, ventral and parallel to the developing gut. These strands contain many large nuclei, most of which will ultimately be contained in egg-cells, but their anterior ends develop into the oviduct leading to the epigyne. The distinction becomes evident a few days later when the future eggs or oogonia come to occupy the centre of the strand and possess larger nuclei than the peripheral cells.

The next change in the oogonia, the formation of primary oocytes, is one of great importance. The division differs from ordinary mitosis in that the chromosomes appear at the equator of the spindle-rays in pairs instead of separately, and disposed at right angles to the equatorial plane instead of lying on it. When the oocytes in their turn divide to form secondary oocytes, these pairs of chromosomes separate instead of splitting. Thus the secondary oocytes have but half the original chromosome number, seven in spiders, instead of fourteen. This reducing division or meiosis is a characteristic stage in the gametogenesis of both sexes of animals and plants.

There is, however, another important feature to be noticed in the production of the secondary oocytes. The egg differs from the sperm in being essentially passive while the sperm is active. Thus the sperm consists almost solely of nucleus with the minimum quantity of investing protoplasm, of which the egg has a plentiful supply. To secure this supply, the division which produces the secondary oocyte is unequal. When the pairs of chromosomes have separated, almost all the protoplasm remains in association with one of the nuclei, the other nucleus is extruded as the " first polar body."

The secondary oocyte now divides by a normal mitosis, but again the protoplasm is unequally distributed and the second polar body is cast out. The other product is the

mature ovum or egg-cell. In some animals the first polar body divides into two cells by ordinary mitosis, so we may sum up by saying that the oogonium gives rise to the egg-cell plus three ineffective cells or polar bodies.

A large proportion of the cytoplasm in the ovum is used as a basis for the yolk, whose function is the nourishment of the developing embryo. Yolk is formed in different animals by different methods and nuclear matter is sometimes concerned in its production. It appears, however, that in spiders the yolk is purely cytoplasmic in origin, though the nutritive material must be originally derived from the haemolymph or "blood" of the spider, and, further back still, from the food. As the ovum grows, small droplets or yolk globules gradually appear, at first near the surface and later inwards. They have a tendency to be formed in radiating lines. The core of unchanged rather granular protoplasm containing the egg-nucleus occupies a more or less central position, and as the egg increases in size, the yolk spheres grow by fusing with one another. During this time the ova are being nourished by copious supplies of surrounding lymph, rich in nutritive substances. These are eventually traceable to globules of reserve protein in the caeca of the food-canal.

As the eggs grow, the abdomen of the spider swells considerably, and now, in some spiders at least, a very remarkable feature appears. The pedicles which attached the eggs to the original ovarian strand disappear, so that the eggs lose their connection with the ovary and are, in fact, lying in the haemocoelic cavity between the intestine and the silk-glands. How, then, can the eggs be laid? It is found that each oviduct becomes perforated, close to its junction with the uterus, and through this small aperture the eggs squeeze themselves in single file on their way to the exterior.

Spermatogenesis

Typical spermatogenesis resembles typical oogenesis in the pairing and halving of the chromosomes. Each

spermatogonium gives rise to spermatocytes, and the final spermatocytes have half the normal number of chromosomes.

There is an important difference between the two sexes in the number of chromosomes. When the spermatogonia divide there is seen to be an extra chromosome, making the total fifteen, in place of fourteen. It must therefore happen that in the pairing of the chromosomes which precedes the reducing division, this extra chromosome must be unmatched, with the further consequence that the final spermatocytes and the spermatozoa are not all alike. Half of them possess seven chromosomes, the others eight. This extra chromosome is known as the X-chromosome or the Sex-chromosome, because it seems to determine the sex of the offspring. The ova are all alike with seven chromosomes : an ovum fertilised by a sperm with seven chromosomes produces a female with fourteen chromosomes in all the cells, an ovum fertilised by a sperm of eight chromosomes produces a male with fifteen chromosomes in its cells. This same difference has been noticed in some insects and in some mammals, including man. The fact that the spermatozoa are produced exactly similarly and in equal numbers destroys many, if not all, of the attractive theories of sex-determination of the Middle Ages—and later.

Spermatogenesis in spiders seems to vary sometimes from the typical sequence, at least in certain species. Professor Warren of Pietermaritzburg, has observed in the spermatogenesis of *Palystes natalius* frequent divisions of the spermatogonia by mere fragmentation of the nuclei, or division by amitosis. But if amitosis is general in spiders, the belief that the several chromosomes are the individual vehicles of particular hereditary characters would have to be modified. At the moment, the situation is further complicated by the description of quite typical spermatogenesis for other spiders. It appears certain, however, that there are two sorts of spermatozoa, some formed typically, and the others smaller and produced by atypical changes. This phenomenon is not unknown in other animals. Abnormal

spermatids have been found in many insects and molluscs and even occasionally in mammals. In all cases, however, there is a proportion of normal spermatozoa which effect fertilisation. Both types may be found in the spermathecae of female spiders, having been placed there by the methods described in an earlier chapter.

Fertilisation

The soft and delicate eggs are laid, as already described, in a quantity of syrupy lubricating fluid. Since the polar bodies are formed within half an hour or so of the oviposition, and since ova do not usually attract sperms until after the polar bodies are formed, it is most likely that the spermatozoa are discharged from the spermathecae into the lubricating fluid at the time that the eggs are laid and that fertilisation occurs almost immediately afterwards.

There is no aperture in the outer egg-membrane or chorion, but at the time of laying this is so soft that it would offer no resistance to the passage of the spermatozoon. The latter, therefore, penetrates the egg at any point, and in eggs laid only half an hour before fixation there can be found a small nucleus between the yolk globules, which is no doubt the sperm-nucleus travelling towards the ovum-nucleus.

Parthenogenesis

The exact significance and value of the nearly universal phenomenon of the conjugation of the gametes is an old problem and one which has not even to-day been satisfactorily solved. There has never been any doubt that, in the majority of cases, fertilisation is an essential preliminary, without which development of the egg cannot occur. The problem is complicated by our ignorance of what, precisely, the ovum owes to the sperm, and also by the existence in some animals of both parthenogenesis and polyspermy.

Polyspermy, or the entry of two or more spermatozoa into an ovum, has not been observed in spiders, but there

are several records of parthenogenesis. If such records are to be regarded as trustworthy, one condition must be fulfilled. Since the female spider can store in her spermathecae all the sperm required to fertilise three or four cocoons of eggs, proof must be forthcoming that the spider has not been mated before capture. The only proof of this is that she shall undergo at least two moults, and so become sexually mature, when in captivity.

The first record of parthenogenesis in spiders was made by Campbell in 1884, on the not uncommon British spider *Tegenaria parietina*. His spider spent most of her life in a bottle and was apparently given no opportunity of meeting a male. She laid a cocoon of eggs, as many virgin spiders will do, and two of these eggs developed into young spiders. These interesting little creatures, however, did not survive for very long. Six years later a second case was recorded, by Damin. His spider was *Filistata testacea*, the females of which are said to be very common in the South of Europe, while the males are much rarer. She underwent two moults while in captivity, never met a male, but laid a cocoon of eggs from which sixty-seven healthy young hatched.

Montgomery, in 1908, kept two females of the famous Black Widow, *Latrodectus mactans*, in circumstances which would test the possibility of parthenogenesis, but none of the eggs hatched. This result was in accordance with the more extensive tests carried out by Blackwall fifty years previously, in which no parthenogenetic young were produced.

An important contribution to the subject has been made by Warren in his recent work on *Palystes natalius*. Of eight females caught and kept by him, four laid eggs which all developed in a perfectly normal way, while the eggs of the other four developed only partially and very slowly. It is suggested that these eggs exhibited a parthenogenetic tendency which varies in intensity in different individuals. This is supported by the fact that a female which Warren reared from the egg, of whose virginity there could there-

fore be no question, laid eggs which were able to undergo the early stages of segmentation.

The only conclusion justifiable at present seems to be that parthenogenesis in spiders is rare, but possible, at least for some species.

Development

The fertilised egg is a spherical mass of protoplasm, the zygote nucleus within but not necessarily at the centre, surrounded by the yolk globules already mentioned, arranged radially around it. Enclosing the whole are two membranes, the vitelline membrane inside and the chorion outside. A thin layer of protoplasm underlies the vitelline membrane and is doubtless in continuity with the central protoplasmic mass containing the nucleus, being joined to it by the fine foam-like protoplasm through which the yolk globules are dispersed.

The first division of the nucleus is meridional and produces anterior and posterior cells ; at the same time the two-celled embryo acquires a bilateral symmetry by the flattening of the future ventral surface. The second division is also meridional, but it is at right angles to the first, and the third is equatorial. The eight-celled stage thus consists of dorsal and ventral layers of four cells each, and is reached in about ten hours from the time of laying. After this the cell-division becomes irregular, and although some workers have been able to recognise a sixteen-cell stage, and even a thirty-two-celled stage, it is generally agreed that irregularity begins after the third division. The small cells travel between the yolk spheres in an outward direction, and when about twenty-eight hours old the egg possesses an approximately complete layer of perhaps a hundred peripheral cells, surrounding the yolk within.

This condition forms a stage which is common to the development of most animals and is known as the blastosphere. In an egg like that of *Amphioxus*, not complicated by large masses of yolk, the blastosphere is made by a very

similar separation of cells as they are produced, and takes the form of a hollow sphere, bounded by a single layer of cells. The formation of the blastosphere is usually taken as marking the end of the simple process called segmentation.

The next stage is one of great importance. The blastosphere consists of a single layer of cells, whereas the bodies of all higher animals consist of cells derived from three embryonic layers. These germinal layers, as they are called, are the epiblast outside, the hypoblast inside, and the intermediate mesoblast separating them. The formation of the layers themselves is of interest because of the importance attaching to them. Adult organs or parts produced from different embryonic layers cannot be considered homologous, even if they have the same function, and must not be taken as evidence of relationship. The Malpighian tubules have already been mentioned in illustration of this. Hence the three germinal layers form a court of appeal from which we may learn much concerning the relationships of different classes of animals.

In a simple hollow blastosphere the next stage consists of a tucking-in of one side until it touches and is surrounded by the other, just as a hollow ball might be pushed in with the thumb. In this way epiblast and hypoblast are formed. But this simple invagination is not possible when the segmentation cavity is filled with yolk, and other methods must therefore be used.

In spiders, the cells which form the ventral surface multiply rapidly at a point near the anterior end, forming an opaque white mass which ultimately projects a little above the surface of the egg. This is called the anterior cumulus. Its cells multiply rapidly, absorb nourishment from the yolk and form first the mesoblast, then the hypoblast. A similar posterior cumulus arises behind the first and ultimately comes into contact with it (Fig. 86). The meeting-point of the two cumuli marks for the first time the division between the cephalothorax and abdomen. At this stage, which is reached after about three days, the egg

is still approximately spherical and the mesoblast is a single layer of cells internal to the ventral surface.

There now appear almost simultaneously four segments of the cephalothorax, and later a fifth segment. Meanwhile the mesoblast within has split into two layers, the space between them constituting the coelom or primitive body-cavity, but this is ultimately obliterated except in the coxal glands and the stercoral pocket.

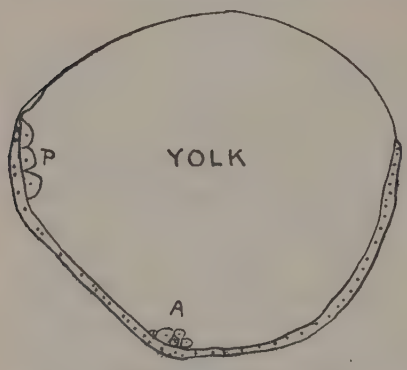


FIG. 86.—Development. An early stage in development of the egg. After Montgomery. A, Anterior cumulus. P, Posterior cumulus.

Appendages now begin to appear on the cephalothoracic segments, at first as small knobs and later elongating until they become obvious cylindrical limbs (Fig. 87). After their appearance, the abdomen, previously represented

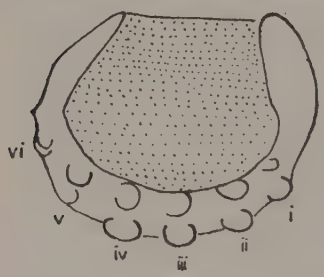


FIG. 87.—Development. Stage showing beginning of limbs. After Montgomery. i, Chelicerae; ii, Palpi; iii–vi, Legs.

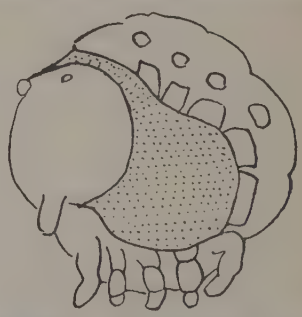


FIG. 88.—Development. Stage showing abdominal segments and limbs. After Montgomery.

only by the posterior cumulus, begins to elongate rapidly, spreading from beneath round the egg until caudal and cephalic regions almost meet. It also acquires a temporary

but very definite segmentation, consisting of from eight to twelve segments. The foremost of these segments disappears very early and never bears a sign of appendages, but on all the others rudimentary limbs appear in the form of small knobs (Fig. 88). Those of the second and third segments become invaginated and form lung-books; those of the fourth and fifth persist as spinnerets; the rest disappear with the segments. Heart, intestine, and nervous system have meanwhile been formed within, and all the other internal structures are gradually established.

If the preceding account has been followed, it will be realised that the embryo spider is formed on the outside of the egg and that it is now bent round it with its ventral surface outside and convex (Fig. 88). This extraordinary position is altered before hatching by a process not generally

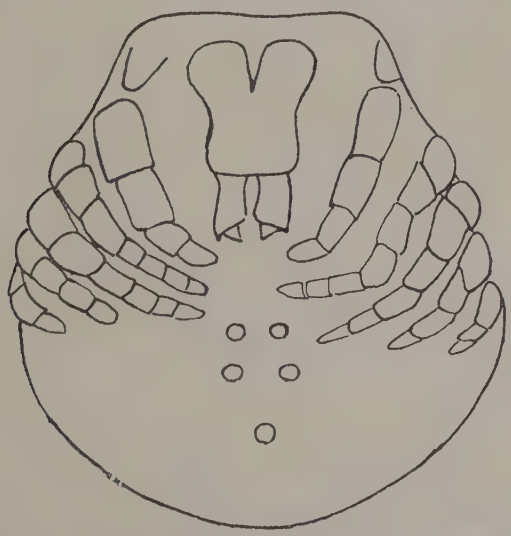


FIG. 89.—Embryology. After reversion. From Balfour.

seen in the embryological development of other animals and called reversion. The mechanical forces which bring about reversion have been variously described and the most likely course of events seems to be as follows. The

sternum widens and therefore shortens, so dragging the abdomen down. Simultaneously the elongating legs, pressing against the harder chorion, force the cephalothorax upwards, so that the bending of the spider is reversed and it becomes convex above and concave below. It is now ready to hatch (Fig. 89).

Hatching

Not less than a fortnight after the egg was laid the embryo bursts the vitelline membrane and chorion by the forward growth and stretching of the cephalothorax. The period varies, however, as might be expected, with the same species in different climates, and with different species everywhere according to their life-history. Eggs laid in the spring or early summer become small independent spiders in the course of a few weeks, while those laid in the autumn do not appear until the next spring. Hatching from the egg by the rupture of its membrane is, however, not the same thing as escape from the egg-cocoon, inside which the small spiders remain for a similarly variable time. At this period of their lives there is some justification for following the practice of the few authors who refer to them as larvae, for they differ in several ways from the adult or even the free-living young spider. Larva is, however, a word with an exact technical meaning and should strictly be applied only to those instances of development in which there occurs a metamorphosis or complete change of outward form and often of habits as well. The newly-hatched spider in the cocoon is not entirely or even conspicuously different from the adult; it is merely incomplete; moreover, its subsequent changes are introduced by an ordinary moulting which differs in no essential from those that follow. The development, in fact, is "direct" at all times and, for these reasons, the word "larva" is not admissible. When it is necessary to distinguish the newly-hatched spider from the spider outside the cocoon, the word "spiderling" might well be used.

The Spiderling

The spiderling, while still within the cocoon, is a particularly interesting creature. At first it is quiescent, but in a few days it begins to move about inside its silk nursery. Warren has described the curious fact that during all this time, even when the spiderling was not moving about, a constant up-and-down movement of all the limbs is to be seen, quite slow but quite continuous. He suggests that these movements have probably a physiological function promoting the circulation of the blood during the development of the vascular system.

By far the most interesting thing about the outwardly normal spiderling is its incompleteness. The spinning glands have as yet scarcely begun to form, so that the young creatures do not waste their substance in the production of silk. If threads were spun at this time, they would merely tend to choke up the cocoon and impede the movements of the occupants. They would be doubly purposeless, for there is no prey to be caught and, even if there were, the spiderling would be unable to eat it. The spiderling cannot feed, for its mouth-parts are still incomplete. For some days, until by moulting it ends its pseudo-larval life, it depends for nourishment on the remnants of yolk which are still present in the gut-caeca. All the spiderling's energy is due to the retention of the yolk, which can easily be seen under a microscope, even as its disappearance from the abdomen can be followed in the gradual thinning of the fat little creature.

The young spiderling is almost entirely devoid of pigment and is therefore nearly transparent; under a microscope the stomach and the diverticula filled with yolk can easily be seen. The proportions are not those of the adult. Most interesting results are being obtained by a sufficiently close study of these spiderlings, which are easily mounted for examination. Spiderlings of different families, including the most specialised, usually show considerable resemblance at this time, and they recall the

adult forms of more primitive types. For example, the coxae of the fourth legs are usually widely separated, and the end of the sternum is produced between them. All the coxae are longer, when compared with the other leg-joints, than in full-grown spiders. In the adult *Epeira* the palpi are quite short and inconspicuous, but in the spiderling from the cocoon they are about two-thirds as long as the legs of the first pair. The result is that at first glance the spiderling seems to have ten legs, in fact, exactly the same appearance as have the Mygalomorphae.

The arrangement of the eyes, which, as already mentioned, is a feature used in the separation of the families and genera, illustrates the same early resemblance of divergent types. For example, the Lycosidae and the Pisauridae are two allied families of hunting-spiders, the Lycosidae being later arrivals in the history of the spider race than the Pisauridae. Their eye-patterns are distinct, but the spiderling Lycosid has the eyes of the Pisaurid.

All the limbs are smooth and colourless, for the spiderling has no hairs or spines. The claws on its tarsi are smooth and devoid of teeth. On the abdomen, the anterior spinnerets are somewhat in front of their final positions. The anal tubercle is prominent, and above it traces of segmentation are still perceptible. A large proportion of the little creature is soluble in caustic potash, showing that chitin is not as yet abundantly present—in fact, the tiny fangs of the chelicerae are almost all that can be recognised after treatment with this reagent.

This stage of the spider's development is brought to an end by its first moult, which usually but slightly precedes the escape of the spiderling from the cocoon. As a result of this first moult, the legs lengthen and a certain degree of colouring appears, but not that of the adult pattern. The silk glands commence to secrete and silk can be spun for the first time, though the alimentary canal is generally still incomplete. Often, too, the eyes only appear at this stage.

Recapitulation

It is obvious that to a very marked extent the developing spider illustrates the important biological fact known as recapitulation. In the embryonic development of most animals, certain features appear which have only a transient existence and vanish before the creature hatches. Thus in spiders, the appearance of both thoracic and abdominal segments has been noted, and of abdominal appendages which are not present when the spider has grown up. The whole of embryology is full of similar instances, but the most striking examples are found among the Vertebrates. The developing vertebrate has at one time a simple tubular heart, pharyngeal apertures like gill-clefts, a notochord, segmented muscles, and so on. All these features are known in the adult states of lower Vertebrates, and their temporary appearance in the life-history of higher Vertebrates can scarcely be explained by any other hypothesis save that of recapitulation. Based upon the theory of evolution, this explanation suggests that their retention is due to the fact that these structures were once possessed by the ancestors of the race, but that they have been lost or repressed in the evolutionary changes which followed. In other words, the embryonic development of an animal is a much abbreviated recapitulation of the historical evolution of its race, or, in Haeckel's form of statement, ontogeny repeats phylogeny.

The recapitulation theory has had a great attraction for some writers, who have extended it beyond justifiable limits. As long as it is confined to the embryonic persistence of important structures, known to have been possessed in primitive ancestors, but disappearing in the later development of the type in question, the theory is on firm ground, but it is hopeless to extend it to include every embryonic character, and to interpret all as inheritances from ancestral conditions. A slavish adherence to the recapitulation theory in its extreme form would lead one to postulate the existence of an ancestral spider which could neither see nor eat.

Moulting or Ecdysis: Regeneration

The young spider, after its escape from the cocoon, becomes an independent individual, and, as explained in a previous chapter, its first care is migration. It is worth noticing that at this time the outstanding feature of the spider's character is its apparent bravery. Apart from the recklessness with which it launches itself upon its first aerial voyage, it exhibits an unhesitating boldness in attacking its prey. These young spiders may be kept in cages and fed on gnats and other small insects. The delicate webs which they spin are all but invisible, but when the gnat intrudes, the spider rushes upon it without hesitation. Sometimes the spider bites the insect before it succeeds in disentangling itself, and then gets carried bodily round the cage, still holding fast. Its whole behaviour suggests vigour and that quality of insurgence which characterises all life.

As the spider feeds it grows, with the result that the rigid chitinous exo-skeleton becomes too tight for its expansion. Since the chitin is not only hard but non-living, it must be cast before an increase in size can take place. This discontinuous growing is not, of course, peculiar to young spiders: it is characteristic of Arthropoda in general, and is necessitated by the non-expansible non-cellular, non-living cuticle. Even at lower levels, as in nematode worms, there is a somewhat similar punctuation, associated with cuticular moulting.

The process of moulting or ecdysis in spiders has been several times described, and indeed it is not difficult to observe it. It is only necessary to keep a sufficient number of immature spiders in cages and to look at them often enough. It is probable that in natural circumstances ecdysis most generally occurs at night, but in captivity it is often performed at a more convenient time.

Ecdysis does not occur without warning. For some days before it is due, the spider refuses food and the colour of the legs darkens until they are almost black. From all

the published accounts and from my own observations, it seems that the position which the spider occupies when moulting is similar in all families, and that, broadly speaking, the process is always more or less the same.

For some time before any visible changes occur, the spider suspends itself upside down, its feet close together and its abdomen supported by a thread from the spinnerets. Its first activity is a raising and lowering of its cephalothorax by bending the legs, and a broadening of the abdomen. This causes the cuticle of the abdomen to split along the middle of the back, and the split gradually extends round the sides of the cephalothorax until it reaches the chelicerae. It usually stops here. The old cuticle soon shrivels off the abdomen and the carapace of the cephalothorax soon falls away. The most tedious part of the operation is the simultaneous extraction of the legs and palpi. The cuticle here does not split, so that the limbs have to be slowly pulled out. This is achieved by a series of heaving movements, assisted by the weight of the spider's body, which gradually extracts them from their old coverings. During this time the spinnerets are still attached by the silk threads, and it is important that the now empty tarsi remain fixed in their original positions. If one of them come adrift, the spider has great difficulty in freeing that limb.

As many as six hundred pulls may be required to remove the legs, and the time occupied by the whole casting of the cuticle varies from fifteen to forty minutes. After the moult the spider is paler in colour and softer in consistency than usual; it is exhausted and rests motionless for some time, but before the new cuticle has hardened it combs itself, particularly its jaws, mouth parts, and under surface with its metatarsi. Possibly this sets the setae in their proper directions.

The period of moulting is a critical time in the spider's life, during which it is quite unprotected. It is therefore not surprising that some species spin a silk chamber all round themselves and cast their cuticle within its shelter. Internal changes begin a comparatively long time before

the actual casting, before, during, and after which the creature is temporarily deprived of several of its faculties—sight, touch, movement, and even for a moment respiration. Wagner, who described the course of the moult as long ago as 1888, stated that a lubricating fluid is secreted to help the process. This seems to have been an error, for under the most favourable conditions no drops of fluid are visible and the limbs seem to be perfectly dry when extracted.

At the time of moulting the spider's power of regeneration is often in evidence. It is a common character of most of the lower animals that they can reproduce lost parts. Higher in the animal kingdom this regenerative power becomes less, until in mammals there is little more than the ability to heal a wound. It has already been mentioned that the spider often escapes from its captors by throwing off a limb. The lost parts grow again beneath the exo-skeleton and at the time of moulting become visible and functional. If the loss occurs shortly before moulting is due, a rudiment only may be produced, but if there is a subsequent moult, a perfect limb results. This accounts for spiders with an apparently asymmetrical set of legs.

Size

Owing to the difficulty of rearing young spiders, there are few records of the number of moults that occur before the spider reaches maturity. It is probable that not less than three and not more than ten changes of integument take place, but the number may depend on the size of the adult and on the circumstances of growth.

The size of the adults of the various kinds of spiders differs within unusually wide limits. The smallest known spiders are probably the members of the Amazonian species, *Ogulnius obtectus* (Fig. 90) of the family Epeiridae. The female of this spider is only one millimetre long ($\frac{1}{25}$ of an inch). The British spiders of the genus *Tapinocyba* are little more than a millimetre long, and the type specimen of the male of *Tapinocyba praecox* is under a millimetre.

Male spiders, as has been noted, are nearly always smaller than the females. On the other hand, the body of the trap-door spider, *Theraphosa leblondii*, is nearly 90 mm. (about 3½ inches) long: and several other members of this sub-order are over sixty millimetres.

FIG. 90.—Ogulnius obtectus. × 40. After Pickard-Cambridge.

It should also be noted that individuals of the same species are not all of the same size. The species of *Tegenaria*, for example, found in sheltered situations in Cornwall are very much bigger than those which live in the north of England. It is frequently noted in reports on collections from certain localities that the particular spiders are larger or smaller than the general run of their kind, and no doubt local conditions alone are responsible for this. I have been told of a *Pholcus phalangioides* caught in England whose legs spanned six inches, an excess of nearly fifty per cent. over the usual size.

It seems also to be quite well established that spiders may sometimes increase in size, even after sexual maturity has been attained, to such an extent that another moulting may be necessary. Thus it may come about that a spider which has been fertilised and has laid her eggs in their cocoon, may afterwards moult. It has even been suggested that in spiders whose mature life occupies more than one year, an annual moult may be a normal occurrence, but there is as yet no definite information on this point. Moulting after egg-laying would seem to be exceptional rather than usual.

Alternatives in Development—Dimorphism

The normal development of the individual spider is a repetition of that of its parents and is similar to that of its brothers, but there are a few species in which alternative types may arise.

One instance of this is the female of a spider already mentioned (p. 159), *Misumena vatia*, which sometimes has reddish streaks on its abdomen and sometimes has not. A much commoner British spider, which is to be found almost everywhere in summer months, is one of the Theridiidae, *Phyllonethis lineata* (Fig. 91). Four or five varieties of this species exist. The typical form has a uniformly yellow abdomen, with a characteristic arrangement of black dots. A common variety, originally described as a distinct

Fig. 91.—Phyllonethis lineata. Variations of pattern.

species, *Theridion redimitum*, has a crimson red loop surrounding the central mark, while in another, rather less common and at first called *Theridion ovatum*, the crimson forms a continuous shield over the whole of the upper side of the abdomen. More rarely still pure white specimens may be found and very occasionally uniformly pink examples occur.

This spider is richer in well-marked varieties than any other, but several possess varieties, often of the familiar melanic type. The spider *Drapetisca socialis* in particular is a species often found on the bark of trees, and specimens vary from a light shade with well-marked pattern to a uniform jet black, on which no pattern is visible.

The problem of the origin and relations of the different varieties of *Phyllonethis lineata* does not seem to have been worked out as yet. All the three commoner types may usually be taken in the same neighbourhood, but it is not known whether the pigmentation is influenced by the surroundings or whether it is an unalterable inborn character.

Among male spiders the phenomenon of dimorphism is in a few species much more pronounced. The best-known case among British spiders is in the little species *Troxochrus scabriculus*. This was described in 1862, and in 1870 another, *Troxochrus cirrifrons*, was discovered and believed to be its close ally. Some authorities maintain that the two are distinct species, others regard them as varieties of one, differing only in the extra tufts of "hair" on the head of *cirrifrons*.

That this view is at least probable is supported by another well-known instance of a similar dimorphism in the American jumping-spider *Maevia vittata*. In this case there is no doubt that there is but a single species, with one type of female and two types of male. The two males are found in equal numbers, and together are about as numerous as the females. One male is uniformly grey and only a little darker than the female, the other is pitch black with yellow legs and carries on the frontal region three tufts of "hairs" projecting forwards. In this respect, therefore, there is a striking resemblance between the two instances of dimorphic species.

The constitution of *Maevia vittata* has been carefully studied by Painter, who finds that the varieties are accompanied by particular chromosomes. The cells of the female spider possess two sex-chromosomes, represented in Fig. 92 by the letter X, and one other chromosome-like body, represented by the letter C. The ova are thus of two kinds, those which carry XC and those carrying X alone. The cells of the grey male possess one X chromosome and one C. Half of its spermatozoa, therefore, carry neither X nor C, one-quarter carry X and C, and one-

quarter X only. The cells of the tufted male carry one X chromosome only, so that half its spermatozoa carry X and half nothing. Their possible unions, producing viable or living zygotes, are shown in Fig. 92.

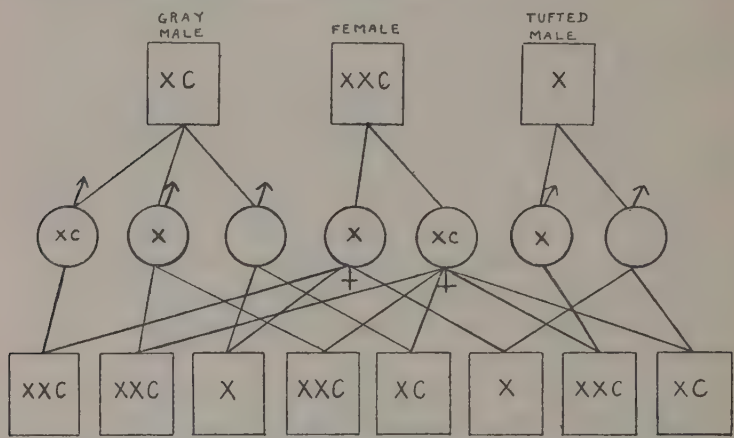


FIG. 92.—Scheme showing relation between dimorphic forms of male Maevia vittata and the chromosomes of the gametes. Circles, gametes; squares, zygotes.

This work of Painter's is of particular interest since it illustrates, for the first time among spiders, that the chromosomes influence the sex and appearance of the individual and its offspring.

ABNORMALITIES IN DEVELOPMENT—GYNANDRY

It is a familiar fact that the customary distinction between male and female organisms is absent from some animals, such as earth worms and snails. These are hermaphrodites, and are able to produce both ova and spermatozoa. Hermaphroditism is unknown among spiders, but the term is sometimes misapplied to abnormal specimens which unite in their bodies some of the characters of both sexes. Such freaks are properly described as gynandromorphs, the distinction being that hermaphrodites are normal and functional members of their race, while

gynandromorphs are rarities, incapable of functioning as either sex.

Gynandromorphs are well known among ants and in the fly *Drosophila*. In the latter case it has been shown that the cause of gynandry is the failure of an X chromosome to keep pace with the others, so that in an early division of the egg it is dropped from one of the cells. This cell and all its descendants have thus one X chromosome fewer than the others; they show male characters, while the rest show female characters. Thus the resultant insect is a mosaic of male and female features.

The subject of gynandry in spiders was treated in a paper by Hull in 1919. The instances which are there described may be classified in three groups, as follows:

1. One side male, the other female (Fig. 93).

FIG. 93.—Gynandromorph Oedothorax fuscus. Left side male, right side female. From Hull, after Kulczynski.

FIG. 94.—Gynandromorph Lophomma herbigradum. Cephalothorax female on left, male on right. Abdomen male on left, female on right. The smaller diagram shows the genital area. After Hull.

2. The same, but one side imperfectly developed before, the other behind.

3. One side male before and female behind, the other side female before and male behind (Fig. 94).

Spiders with these peculiarities are very rare indeed, and probably less than a score have ever been found. It is clear that they are all of a mosaic type, probably due to abnormalities in the behaviour of the X chromosome.

CHAPTER XIII

FOSSIL AND PRIMITIVE SPIDERS

THERE is always an intrinsic interest attaching to the early history of a race, whether it be mankind or some group of animals. The interest is due partly to our natural curiosity about the beginnings of things, and partly to the fact that our attempts to read these early histories are necessarily mixtures of deduction and conjecture, and thus have the appeal which the solving of a puzzle must always possess.

In Biology the early histories of the different classes of animals gain an additional importance from the light they throw on our interpretation of evolution. This is obvious, because it is only from a study of the bodies and skeletons of animals which died in far-off days that we can hope to obtain an undeniable proof of the fact of evolution itself, as well as an indication of the path it has taken in the group we happen to be studying.

THE GEOLOGICAL RECORD

These bodies and bones which the rocks have preserved for us in the form of fossils, are as words on the pages which make up the geological record of animal life. It is when we remember how small a proportion of the animals of the past can have died in circumstances suitable for the production of fossils, and how small a proportion of the existing fossils have as yet been unearthed and examined, that we realise that the geological record must be very incomplete. Ideally, it would be a story of surpassing interest and profound value; in practice we cannot hope for more than a

few hints. These, however painfully, we must try to piece together.

In seeking to determine the geological history of the order of spiders, we are faced with this incompleteness in an extreme degree. Spiders' bodies are too soft to provide good material for forming fossils among the stratified rocks, with the result that in such situations the preservation of spiders has occurred but rarely. There is, however, another way in which not only spiders but also insects and other invertebrates have been preserved for us, and this is in amber. Amber or succinite is a compound of carbon, hydrogen, and oxygen, but is not quite homogeneous in character. It is a fossil resin, exuded from trees of the Eocene and earlier Oligocene periods, and is found on the shores of a large part of the Baltic and the North Sea.

The spiders preserved in amber belong to a much later period of the world's history than those found in rocks, and, as it is necessary to understand this, the following table is given as a guide :—

Primary or Paleozoic Epoch.	
Cambrian Era.	Earliest fossils.
Ordovician Era.	
Silurian Era.	Fishes.
Devonian Era.	
Carboniferous Era.	Amphibia.
Permian Era.	Reptiles.
Secondary or Mesozoic Epoch.	
Triassic Era.	
Jurassic Era.	Birds.
Cretaceous Era.	
Tertiary or Cainozoic Epoch.	
Eocene Era.	Mammals.
Oligocene Era.	
Miocene Era.	
Pliocene Era.	
Pleistocene Era.	Man.

It will be seen that the world's past is divided into three major epochs, each of which is subdivided into a number of eras, corresponding to defined systems of rocks. The length of time, measured in years, occupied by these epochs is a somewhat controversial subject on which it is difficult to secure agreement. In any case the total age is so enormous that the mind does not really appreciate it. It may be said that life has existed on the earth for five hundred million years, but in reality all that this conveys is " a very long time."

Paleozoic Spiders

In the Paleozoic rocks, spiders occur in the Carboniferous system. The first known fossil spider was discovered in 1866 in the argillaceous shale of coal formations at Kattowitz, in Upper Silesia, and has been named *Protolycosa anthrocophila*. It is a wonderfully fine and almost entire specimen, its dark body well defined against the greyish background of the shale. The separate joints of the legs and palpi are clearly to be seen and even the setae which covered them, while there is no mistaking its most striking feature—the segmentation of its abdomen. The name *Protolycosa* was a somewhat unfortunate choice, due to a superficial resemblance of this unique spider to the modern Lycosidae. Its segmented abdomen proclaims what the rest of its visible structure supports—the fact that it is not a distant relation of those primitive spiders which have persisted till to-day as the Liphistiidae. For instance, its legs have the same relative lengths as have the legs of the Liphistiidae, and the close approximation of its eyes is another primitive feature.

Another spider, similar in many ways to *Protolycosa*, was discovered in Carboniferous strata in Illinois in 1874. This was called *Arthrolycosa antiqua*, as it was regarded as belonging to a different genus. Thirty-seven years later, in 1911, three fossil spiders were described from Dudley, Worcestershire. One of these evidently belonged to the same genus, which was thereby shown to have had a

distribution embracing the northern halves of both hemispheres. A third species, *Arthrolycosa danielsi*, was added to the genus in 1913, also from Illinois. Five other fossil spiders have been described as species of Arthrolycosa, but they have been transferred by Petrunkevitch to a new family, Arthromygalidae. Four other genera, each at present consisting of a single species, complete the list of Paleozoic members of the primitive sub-order Liphistiomorphae.

1. Arthrolycosa antiqua Harger.	1874.	Illinois.
2. Arthrolycosa danielsi Petrunkevitch.	1913.	Illinois.
3. Protolycosa anthracophyla Romer.	1866.	Silesia.
4. Eocteniza silvicola Pocock.	1911.	Worcestershire.
5. Arthromygale carbonaria Kusta.	1888.	Bohemia.
6. Arthromygale fortis Fritsch.	1904.	Bohemia.
7. Arthromygale beecheri Fritsch.	1904.	Bohemia.
8. Arthromygale lorenzi Kusta.	1888.	Bohemia.
9. Arthromygale palaranea Fritsch.	1904.	Bohemia.
10. Racovnicia antiqua Kusta.	1888.	Bohemia.
11. Geralycosa fritschii Kusta.	1888.	Bohemia.
12. Perneria salticoides Fritsch.	1904.	Bohemia.

It is clearly of great interest to notice that this sub-order, at present confined to the East Indies and Japan, was evidently the dominant type of aranead population in Paleozoic days. It possesses, so far as we know, at least two genera in America and five in Europe.

No Paleozoic remains of the Mygalomorphae have been discovered in either continent, and until lately none of the most specialised sub-order, the Arachnomorphae, had been discovered. This led to the assumption that these sub-orders arose during the secondary or Mesozoic epoch, in which case they might have been nearly coeval with mammals. In 1904, however, several fossil spiders were discovered in the coal measures of Nyran, Bohemia, and two of these are Arachnomorphae. The names by which they are now known are *Eopholcus pedatus* and *Pyritaranea tubifera*. These are extinct species, whose descendants to-day have become so modified that they are placed in different genera, and they are of particular interest as showing that spiders, of even the highest sub-order, were already in existence in the Paleozoic epoch. For thirty-eight years it had been believed that only spiders of the

Liphistiomorph type were in existence at that early period of the earth's history.

Another fossil Arachnomorph spider, which came to confirm this discovery, was the third of the fossils from Dudley. This was another extinct genus, and the spider was called *Archeometa nephilina*. Its most characteristic feature is the fact that its second pair of legs are longer than the fourth pair.

Existing knowledge of Paleozoic spiders may therefore be summarised by saying that the dominant types were in every essential similar to the Liphistiomorphae of to-day, and that they were apparently widely distributed over the land. In saying this, it must be remembered that there is as yet no information of the contemporary spiders from the southern parts of the world. Spiders of the Arachnomorph type were perhaps fewer in number, perhaps more limited in distribution, but our present knowledge of them is not sufficient to warrant any definite conclusions.

The Paleozoic Arachnomorphs may be tabulated thus :

1. Eopholcus pedatus Fritsch.	1904.	Nyran.
2. Pyritaranea tubifera Fritsch.	1904.	Nyran.
3. Archeometa nephilina Pocock.	1911.	Dudley.

No Mygalomorph spiders have as yet been discovered in either Paleozoic or Mesozoic strata. It is therefore necessary either to suspend judgment on these or to make the assumption that they did not arise until Tertiary times. This is unlikely, for the Mygalomorphae of to-day possess a primitive type of structure which allies them more closely to the Liphistiomorphae than to the Arachnomorphae, and if primitive Arachnomorphae were existent in Paleozoic times, probably Mygalomorphae were in existence too.

Mesozoic Spiders

Knowledge of the spiders of the Mesozoic epoch is not so full, and indeed for many years no Mesozoic spider was known. The Oolitic limestones of Pappenheim, Bavaria, are famous both for the fineness of grain, which makes

them valuable for lithography, as well as for the number and beauty of the fossils they contain. These include many insects, among other animals, and four species of spiders have also been discovered.

This scarcity of records from the Mesozoic rocks is unfortunate. That spiders were numerous at this time may be deduced both from their relative plentifulness in the other two epochs, and from the number of insects and other remains which indicate an environment quite suitable for the spider's mode of life. Circumstances, however, were perhaps not favourable to fossilisation, and at present the scarcity of Secondary spiders must be attributed to the same Chance which renders all geological records so imperfect.

Cainozoic Spiders

Of the Cainozoic or Tertiary epoch there is, however, a very different story to relate. Tertiary formations have yielded comparatively large numbers of fossilised spiders, from the following chief localities :—

1. Germany	Rott.	Miocene.
2. Switzerland.	Aringen.	Miocene.
3. Provençe.	Aix.	Eocene marl.
4. Isle of Wight.	Cowes.	Eocene limestone.
5. Colorado.	Florisant.	Eocene.

It will be seen that all these places lie north of the equator and that our knowledge of southern forms remains a blank.

An examination of the fossils found shows that Tertiary strata have yielded nearly three hundred species of Arachnida, of which over two hundred and twenty are spiders, the remainder being scorpions and other orders.

The Carboniferous type of Liphistiomorph spider is seen to have persisted in Europe until the Oligocene era. Mygalomorphae have been found in the Tertiary rocks of both America and Europe, the latter including a species, *Eoatypus woodwardii*, from the Eocene of Garnet Bay, Isle of Wight.

Altogether, at least 222 species of Tertiary spiders are

known, included in seventy-one genera. Sixty-six of these genera have been found in Europe and thirteen in America, eight being therefore common to both. Thirty-five European and two American genera are extinct, but the remaining thirty-four genera have living representatives, unaltered from those remote times. Of the European species 168 have been found in amber and forty-one in stratified rocks.

When the prehistoric faunas of Europe and America are compared, it is found that in Paleozoic times Europe was apparently the richer in Arachnomorphae. To-day this sub-order is far more numerous in America than in Europe. By Tertiary times, a balance was to some degree maintained. A multitude of forms, including many which have undergone but slight modification since that date, had a widespread distribution over the northern hemisphere. There was then, as there is now, a general correspondence between the fauna of America and Europe, for the same families are represented in the stratified rocks, and, to some extent, among the amber species.

The antiquity of the spider race, even in its present form, is therefore very great. Its pedigree stretches back to the time when our present-day coal was growing in the forests as fern-like trees, long before mammals or birds or even the majority of the reptiles had appeared on the earth.

Primitive Spiders

In this chapter, and in various other places, the Liphistiomorphae have been referred to as primitive spiders, without further describing them or stating the evidence on which their claim to a primitive position is based.

A primitive animal is biologically of greater interest than another because it represents a "missing link," or because it is a present reminder of a bygone age. The structure of a primitive animal differs from that of its nearest living relatives in a number of features which, for various reasons, are considered to be of an earlier origin, and hence it furnishes living evidence of the course that

evolution has taken in the group to which it belongs. Moreover, the material providing the evidence is usually obtainable in a fresh state and in quantity, so that it can be dissected, and these are properties which are not shared by the fossil remains on which the geological record rests. These are the reasons for the emphasis laid on the descriptions of the structure of such familiar primitive animals as *Scyllium* the dogfish, *Amphioxus* the lancelet, and *Peripatus*. The well-remembered "worst journey in the world," the five-weeks' expedition of Dr. Wilson, Bowers, and Cherry-Garrard from Cape Evans to Cape Crozier during the Antarctic winter of 1911, was made for the purpose of securing embryos of the Emperor Penguin, the nearest living approach to the primitive bird.

Two difficulties attend the consideration of the biological significance of a primitive animal. The first of these is generally our comparative ignorance of the directions in which evolution has travelled. It is not as though the past history of any race were a ladder-like ascent of types, or linear progress in which the more specialised examples of one group ultimately gave rise to the less specialised examples of the next. It is more probable that the generalised examples of a group have produced, on the one hand, the specialised examples of that group, and on the other, the primitive members of the next higher group. When a sufficient number of the primitive types have become extinct, the survivors get more or less isolated and the task of discovering their origins and relationship becomes proportionately harder.

The second difficulty is to distinguish between the primitive and the specialised characters of the same animal. Rarely can a type exist for geological ages without acquiring specialisation in one way or another, which, as it were, compensates for its simplicity elsewhere. In other words, it evolves, responding to the impress of environment upon its innate tendency to variation, and it is therefore important to realise that a primitive animal is seldom found to be primitive, lock, stock, and barrel. Further, while an

organ or a part may have all the appearance of simplicity, a study of its development may show that, instead of being primitive, it has retrogressed from some more elaborate condition.

History of the Liphistiidae

Primitive spiders constitute a sub-order with a single family, the Liphistiidae. The first species was described under the name of *Liphistius desultor* by Schiödte in 1849, from a mutilated specimen, whose abdomen had been slit open and stuffed with cotton wool. Pickard-Cambridge in 1875 gave a description of an uninjured example and believed it to be a different species, since Schiödte had been unable to discern the spinnerets of his specimen. Another description of a perfect example was given by van Hasselt in 1879, under the name of *L. desultor*. In 1890 Thorell, of Upsala, pointed out that van Hasselt's species was different from Schiödte's original *L. desultor*, while Cambridge's *L. mammillanus* was identical with it. He proposed the name of *Liphistius sumatranus* for van Hasselt's spider. In 1897 Thorell described a third species of the same genus, named *Liphistius birmanicus*.

In the first volume of the *Histoire Naturelle des Araignées*, Simon pointed out that the specimen in his own collection differed in several ways from all of these, and in the supplement to the second volume, founded upon it a new genus, *Anadiastothele*.

Within recent years, two species have been added to the genus *Liphistius*. These were described by Abraham. Yet another species was discovered in Japan and was referred to a new genus, *Heptathela*. There are, therefore, at the present time seven species of this sub-order, included in three genera. This elaboration of the original species into several closely allied genera is precisely what has occurred in the histories of both *Amphioxus* and *Peripatus*, and does not in any way detract from their general significance. Indeed, this separation is of value because it emphasises the fact, already referred to, that the surviving

primitive animals are not necessarily without elaboration of their own.

Characters of the Liphistiidae

In many ways these spiders recall those of the family of Ctenizidae or trap-door spiders. This is particularly evident in the general outline, in the structure of the cephalothorax and chelicerae, and in the form of the mouth parts, palpi, and legs. At the same time the appearance of the abdomen and spinnerets proclaims the family to be obviously different from all others.

The external features in which *Liphistius* shows its primitive nature most plainly are :

1. The position and number of its spinnerets.
2. The segmentation of its abdomen.
3. The grouping of its eyes.
4. The shape of its sternum.
5. The lengths of its legs.

The usual position for the spinnerets is, of course, at the end of the abdomen, close to the anal tubercle. In *Liphistius* the spinnerets are placed in the middle of the lower surface, a position which more clearly indicates their analogy to the abdominal appendages of other Arthropoda. All other spiders have six or fewer spinnerets, while *Liphistius* alone has eight, arranged in four pairs, constituting the endopodites and exopodites of the fourth and fifth abdominal segments. In the Japanese species, *Heptathela kimurai*, the two inner spinnerets of the posterior group fuse into one, so that there are apparently seven spinnerets.

The segmentation of the abdomen is equally striking. In Chapter I it was stated that this part of the body of Arachnida consists, or originally consisted, of twelve segments, of which the first is the waist or pedicle. In *Heptathela* all twelve segments are visible and each is covered above by a distinct shield or tergite, composed of

chitin and of a leathery consistency. In the descriptions of the other Liphistiidae, nine or ten tergites are mentioned. The first one, above the pedicle, is either overlooked or not included in this count, and these six species seem not to have the large twelfth tergite over the anal tubercle. Simon suggests that these plates may not represent segmentation, but that they result from the division of a dorsal shield similar to that possessed by the genera *Tetrablemma* and *Hexablemma*, and some members of the family Oonopidae.

This is a point which cannot easily be decided, but there is much in favour of the segmental nature of these tergites. A segmented abdomen would ally *Liphistius* to *Protolycosa*, the primitive spider of Carboniferous strata, described above. It would also ally spiders as a whole to the Pedipalpi, another order of Arachnida, an alliance which the Dudley fossil spider *Archeometa nephilina* to some extent supports. Moreover, since the abdomen of all spiders whose embryonic development has been studied passes through a segmented stage, it is reasonable to suppose that the segmented state is a primitive one, and that the dorsal shield of the Oonopidae is a survival which has lost its metamerism, like the rest of the abdomen.

The shape of the abdomen of most of the Liphistiidae tends to become almost spherical, and this is certainly not a primitive form. In all living spiders, the more primitive types have a low cylindrical abdomen, while the spherical form is characteristic of the highest families, the Linyphiidae, Theridiidae, and Epeiridae. It is, perhaps, unwise to stress this point, because of the difference in the constitution of the abdomen in the two sub-orders. The spinnerets of the Arachnomorph spiders appear to belong to one of the later segments, but as a matter of fact they still belong to the fourth and fifth segments. The sixth to the twelfth segments which form the posterior half of the abdomen of the Liphistiidae are much reduced in the Arachnomorphae and form no more than the small anal tubercle. In any case the spherical abdomen of *Liphistius*

is a character in which it shows a specialisation of its own and a departure from the primitive type.

The taxonomic value of the grouping of spiders' eyes has already been mentioned. The course of evolution seems, roughly speaking, to have been a gradual separation of the eyes from a close approximation around and upon the ocular tubercle, so that they become spread over a larger area of the cephalothorax. The retention and elaboration of the ocular tubercle in some of the male Linyphiidae (Fig. 3) is a secondary specialisation, and the reduction of the number of eyes to six, four, two, or none in a few other families seems to be a degenerate rather than a primitive condition. The eyes of *Liphistius*, eight in number, are all situated upon a small pinnacle, and it is probably reasonable to regard this as a primitive condition (Fig. 95). It is interesting to perceive that the median anterior eyes are much smaller than the others. This unusual occurrence has been referred to in a previous chapter; it is an arrangement which is much more common in the southern hemisphere than in the northern, and might perhaps be taken to indicate one of the centres of origin of the spider race.

FIG. 95.—Eyes of Liphistius malayanus. After Abraham.

The sternum of the Liphistiidae is long and narrow. This is a very unusual shape among living spiders: a few six-eyed spiders show somewhat the same shape, but the elongation is not so marked. The nearest approach to the Liphistiid shape is probably that of the Australian trap-door spiders of the genus *Dolicosternum* (Fig. 96), but until more is known of the genealogy of the order of trap-door spiders it is difficult to estimate the significance of this resemblance. It is, however, probably justifiable to assume that a long narrow sternum is more closely allied to a type with a series of segments than is a shorter form.

Liphistius is very unusual in the relative lengths of its legs. In all seven species the fourth pair are the longest

and the first pair are the shortest. The second pair are sometimes shorter and sometimes longer than the third pair. In this respect, as in its segmented abdomen, *Liphistius* recalls *Protolycosa*, in which the relative lengths are 4, 3=2, 1.

The underside of the abdomen of the Liphistiidae is characterised by two very large segmental plates of chitin.

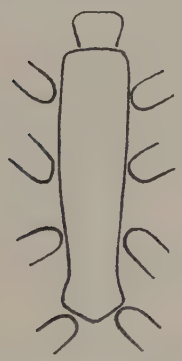


FIG. 96.—Sternum of Dolichosternum. After Rainbow.

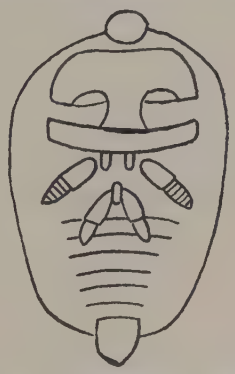


FIG. 97. — Heptathela kimurai. Underside of abdomen. After Kishida.

The later segments are not so large nor conspicuous (Fig. 97). The two large plates cover the two pairs of lung-books and the genital opening. The possession of two pairs of lung-books and the absence of spiracular tracheae constitute a primitive feature, shared by the Liphistiomorphae and the Mygalomorphae.

The female genital aperture has no trace of the outer epigynum, described in a previous chapter, which occurs in all other spiders. All that is visible is a pair of spermathecal apertures at the sides of the hind edge of the plate covering the second segment.

The palpal organ of the male is, naturally, a feature to which one turns in expectancy, for the multitudinous forms which this organ takes throw much light, as we have already noted, on the relationship of the different families.

The most remarkable condition is that shown by the

Japanese species *Heptathela kimurai*. Here the bulb-like receptaculum seminis is completely absent. The tarsal joint of the palp is somewhat swollen, and has very much the appearance of the organ of other male spiders during their penultimate moult. The inner side of this joint is provided with two rows of spines, six or seven spines in each row (Fig. 98), surrounding a space in which the drop of semen is conveyed. Anything more primitive than this literally spoon-like arrangement it would be hard to imagine: indeed, in several ways the Japanese species seems to be even more primitive than those of the Malay Peninsula. The males of both *Liphistius birmanicus* and *Liphistius batuensis*, however, possess palpal organs which, though simple, are more reminiscent of the ordinary types. The

FIG. 98.—Heptathela kimurai. Male palp. After Kishida.

organ projects as a stout blunt point from the very position it would be expected to occupy if it be supposed to have been derived from the palpal claw. This terminal position of the palpal organ is found in most of the trap-door spiders, but in practically none of the highest sub-order, the Arachnomorphae. The retention of a terminal claw by the mature male of *Heptathela* is unique and is not the least remarkable feature of that spider.

INTERNAL STRUCTURE OF THE LIPHISTIIDAE

The only described dissections of the Liphistiid spider are those of Buxton, who, in 1923, cut sections of four specimens of *Liphistius batuensis*. Petrunkevitch has also cut sections of the same species, but has given no account of his results. The description given above of the external features might lead one to suppose that further evidence of

the primitive character of the Liphistiidae would be obtained from its internal structure. It is remarkable that this is not the case, yet the negative results are valuable from a biological point of view.

Buxton was particularly interested in the coxal glands, which show, more than any other internal organ, an evolution of form among the different families. He found that the coxal glands of the Liphistiidae resemble those of the Mygalomorphae or trap-door spiders in every respect. They are not in any way more primitive.

Again, in a very young specimen of a trap-door spider, *Chilobrachys*, from Sumatra, Buxton discovered five pairs of transient abdominal ganglia, a temporary vestige of the vanishing abdominal nerve-chain. One might expect to find these ganglia persisting in the Liphistiidae, but there is no trace of them ; and at present there is no evidence that they persist any longer in *Liphistius* than in any other spider.

The other organs of *Liphistius* show no peculiarities indicative of a more primitive character than the Mygalomorphae.

These results are of great interest because they show that the Liphistiomorphae are much more closely related to the Mygalomorphae than these are to the Arachnomorphae. They tend to correct the impression, which a study of the external characters alone might give, that *Liphistius* and its allies are very primitive spiders indeed. Clearly they are not : they are very important spiders to the zoologist, but they are some way removed from the Archearanead.

Habits of the Liphistiidae

All the earlier species of the Liphistiidae were described from dead specimens, and even Kishida, who apparently finds *Heptathela kimurai* common enough from South Kinshiu to the Loochoo Archipelago, has published no information as to its habits. Abraham, the discoverer of

Liphistius batuensis, has told us more; but it should be remembered that his species lives in the Batu Caves, Selangor, and that its mode of life may not be shared by its allies, which presumably live in the open jungle.

Abraham's spider spins a silk tube, three or four centimetres long upon the vertical sides of the cave. At the bottom of the tube the egg-cocoons are laid, in a cavity which is separated from the tube above by a fine sheet web. A trap-door, consisting of a simple flap of silk, closes the tube, which is fixed to the wall by a number of radiating threads. The trap-door and the tube are covered with particles of sand so that they come to resemble a piece of rock on the side of the cave. This resemblance, if it be

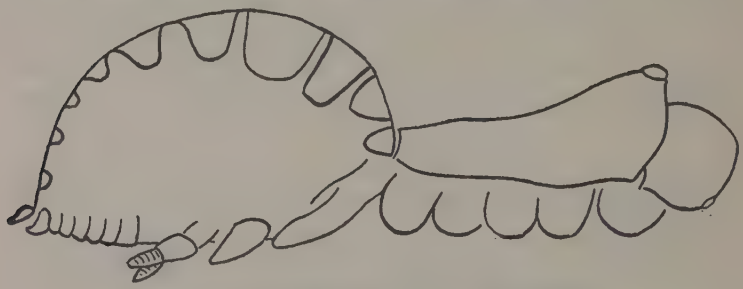


FIG. 99.—Heptathela kimurai. After Kishida.

protective, by making the tube inconspicuous, is rather remarkable since the spiders live some way from the cave-mouth, in the dark. Perhaps the sand masks the feeling of the silk, and thus deceives predatory wanderers.

The remains found in the nests indicate that this spider feeds chiefly on grasshoppers. These it would obtain by hunting along the cave walls, and it apparently takes them back to the nest to devour them in safety. From this fact, together with the coating of the tube with sand, its closure by a trap-door and the nervous behaviour of the spider, it is quite evident that, even in the darkness of the caves, there is some enemy against whom the spider must be perpetually on guard.

When captured by Abraham, the spiders were all

crouching in their tubes, with the doors just ajar, as if they had been driven home in fear on the approach of the intruders. If the hand was brought near the tube, the door was at once closed tightly and held down from within —the spider's last hope of escape.

It is much to be hoped that the Liphistiidae will one day receive the close attention they deserve. Their own interrelations might teach us much, for the Japanese form is clearly more primitive in some ways, and yet in the degeneration of its median spinnerets and the elevation of the cephalic region it has undergone specialisations peculiar to itself. The internal structure, the habits, and the development are all well worth investigation: at present our knowledge is scanty and is scattered over a number of years and a wide range of publications.

In conclusion, the following complete classification of both recent and fossil forms may be not without interest, and will serve as a summary of the chapter.

Sub-order **LIPHISTIMORPHAE** Petrunkevitch

(=Arthrarachnae Haase, =Mesothelae Pocock, =Verticulatae Dahl.)

Abdomen segmented. Not much more than two posterior abdominal segments lost. Anal tubercle separated by a considerable space from the spinnerets.

Family LIPHISTIIDAE

Recent. Tarsi with three claws, the superior claws with 2 or 3 teeth.

Sub-Family LIPHISTIINAE

Four lateral spinnerets, each consisting of two segments; the distal segment with a number of false articulations.

Group LIPHISTIIAE

Two pairs of median spinnerets,

Genus *Liphistius*. Schiödte

1. L. desultor Schiödte (=L. mamillanus Camb.).
2. L. sumatranus Thorell (=L. desultor v. Hass.).
3. L. birmanicus Thorell.
4. L. batuensis Abraham.
5. L. malayanus Abraham.

Group HEPTATHELEAE

Three median spinnerets.

Genus *Heptathela*. Kishida

6. H. kimurai Kishida.

Sub-Family ANADIASTOTHELINAE

Four pairs of spinnerets, each consisting of a single segment only.

Genus *Anadiastothele*. Simon

7. A. thorelli Simon.

Family ARTHROLYCOSIDAE

Carboniferous. Eyes on a tubercle. Claws unknown.

Genus *Arthrolycosa*. Harger

8. A. antiqua Harger.
9. A. danielsi Petrunkevitch.

Genus *Protolycosa*. Romer

10. P. anthracophyla Romer.

Genus *Eocteniza*. Pocock

11. E. silvicola Pocock.

Family ARTHROMYGALIDAE

Carboniferous. Eyes in two rows. Claws two, without teeth.

Genus *Arthromygale*. Petrunkevitch

12. A. carbonaria Kusta.
13. A. fortis Fritsch.
14. A. beecheri Fritsch.
15. A. lorenzi Kusta.
16. A. palaranea Fritsch.

Genus *Racovnicia*. Kusta

17. R. antiqua Kusta.

Genus *Geralycosa*. Kusta

18 G. fritschii Kusta.

Genus *Perneria*. Fritsch

19. P. salticoides Fritsch.

CHAPTER XIV

THE TRAP-DOOR SPIDERS

TRAP-DOOR spiders were discovered by Patrick Browne in Jamaica nearly two hundred years ago, and have since been found to be a numerous group, including about a thousand species, widely distributed throughout tropical and sub-tropical countries. Their structure is so different from that of other spiders that as long ago as 1802 Walckenaer separated them as a "tribe" which he called les Theraphoses. He included, however, the family Filistatidae in the same group. Thorell, in 1869, included them in a sub-order which bore the same name, Territelariae, as the corresponding family of Latreille. The Territelariae included a family Theraphosidae and a family Liphistioidae. Simon's corresponding group in his great *Histoire Naturelle* of 1892 was the sub-order Araneae Theraphosae, in which he placed also the Liphistiidae. Dahl, in 1913, followed Latreille in distinguishing the group by its possession of four lung-books, and in his sub-order Tetrapneumones therefore included the family Hypochilidae, which in other ways does not resemble the rest very closely. In the most recent classification, Petrunkevitch has removed both the Liphistiidae and the Hypochilidae to more suitable positions, and called the sub-order by Pocock's name, Mygalomorphae.

FEATURES OF THE MYGALOMORPHAE

The cephalothorax of these spiders is nearer a square shape than that of others, with little narrowing in the

cephalic region. The median groove or fovea is transverse and is either procurved, with the concavity forwards, or recurved, with the concavity backwards. The eyes are usually closely grouped upon a small ocular prominence and are eight in number in nearly all genera.

The chelicerae afford the readiest means of recognising the sub-order (Fig. 100). Their basal joints project forwards and are able to move sideways only to a slight extent. Their normal action is to strike downwards, so that the fangs pierce the prey from above and move through it in parallel directions. This is in direct contrast to the chelicerae of other spiders, which pierce sideways, and meet in the middle of the transfixed prey. The distal end of the first joint of the chelicerae is in many species provided with a number of teeth forming an efficient rake or rastellus. This is used in excavating the burrow.

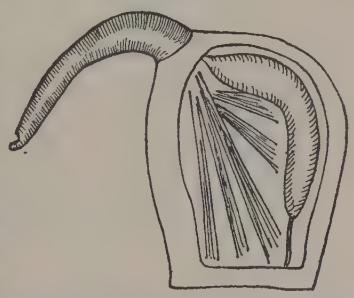


FIG. 100.—Chelicera of a Mygalomorph Spider, dissected to show poison-gland. After Pawlowsky.

The palpi are very like legs in appearance, and are much longer in proportion than is common among spiders. The male organs are terminal in position and simple in structure. The first, or coxal joint of the palp is not provided with the endite or maxilla which forms an important part of the mouth in other spiders. The lung-books, as already mentioned, are four in number. There are also four spinnerets, instead of six. The persistent spinnerets are those of the anterior and median pairs; the posterior pair being absent, save in the family Atypidae and in a few isolated genera.

The abdomen differs slightly in appearance from that of other spiders, for it lacks the colulus, or small tubercle in front of the spinnerets. It is also different in constitution. The heart of the Mygalomorphae possesses four

pairs of lateral ostia instead of three, and is held in position by eight ligaments instead of six.

This makes it probable that one more segment is persistent in the abdomen of the Mygalomorphae than in the Arachnomorphae, that there are six in the former and five in the latter. There is, at present, no embryological evidence which affords definite proof of this view, but other facts are in its favour. If it be accepted, it makes the three modern sub-orders of spiders much more distinct and, moreover, much more naturally separated than in any earlier classification.

Sub-order Liphistiomorphae,	10–12	abdominal	segments.
Sub-order Mygalomorphae,	6	,,	,,
Sub-order Arachnomorphae,	5	,,	,,

Habits of the Mygalomorphae

The habits of these spiders are far from being completely known, partly because many of them are active only at night, and are unusually well concealed during the day. The habits which are known are of great importance, because there is a close connection between them and the structure of the legs, the mouth-parts, and the spinnerets. Habits may thus be taken into account, both in classifying and in considering the evolution of spiders. This will become more evident in the next chapter.

Among the Mygalomorphae there are wandering species, who hunt their prey in the open and take their rest in any chance shelter, under stones or the fallen branches of trees; while others make very simple excavations, lined with but little silk, or even unlined. More skilled diggers excavate deeper holes in the ground, which contain a silk tube and which may or may not be closed with a trap-door, while a few do not burrow at all, but spin their tubes entirely above the ground or weave a web which closely resembles the tube-and-sheet web of the Agelenidae.

These habits have probably arisen by divergence in two

directions from the habits of a primitive ancestor. Some of the descendants specialised in digging and in making trap-door nests. These species possess the rake or rastellus on the chelicerae, with which the digging is done; they have but a slight covering of hairy setae and retain three claws on their tarsi. The most typical family of this tribe is the Ctenizidae. The Migidae represent a further development, and the Atypidae form a family acclimatised to colder regions. The Paratropididae also belong to this group, but nothing is known of their habits.

Other descendants took to hunting. They lost their median tarsal claw and acquired more setae on their legs and bodies. The family Barychelidae includes the species which are in a transitional stage between the burrowers and the vagrants. The Theraphosidae is the typical family of this group. These two families are the only ones which possess claw-tufts, and for this reason they are grouped together, and separately for the other six. The Dipluridae and the Pycnothelidae, which were originally one of their sub-families, are two families which stand apart in several ways from the rest. They spin tubular webs.

There are, therefore, eight families of the sub-order Mygalomorphae, whose chief characters are expressed in the following table :—

	Number of claws.	Number of spinnerets.	Rastellus.
1. Ctenizidae . .	3	4 or 6	Present.
2. Migidae . . .	3	4	Absent.
3. Atypidae . . .	3	6	Absent.
4. Paratropididae . .	2	4 or 6	Absent.
5. Theraphosidae . .	2	4	Absent.
6. Barychelidae . .	2	4 or 2	Present.
7. Dipluridae . .	3	4 or 6	Absent.
8. Pycnothelidae . .	2	4	Absent.

The Paratropididae from the Amazon, and the Pycnothelidae from Brazil, are small families of relatively little importance. The rest deserve fuller consideration.

The Makers of Trap-doors

These are the spiders which owe their popularity to the perfection of their architectural skill, and include the most practised diggers and makers of trap-doors.

The digging is carried out solely by the chelicerae, which, as already noted, are provided with a rake. With this rake small particles of the earth are dislodged, and worked into a ball. This may be carried in the spider's jaws and dropped outside the burrow, or it may be cast up by the strong hind legs, which are sometimes armed with rows of spines adapted to this function (Fig. 101). The sides of the burrow are coated with a plaster, made of earth and saliva, firm enough to isolate it completely from the surrounding earth and able to stop water from soaking in. Within this is a silk lining. The lining is generally fixed to the sides of the burrow, but is sometimes found lying quite freely, and sometimes it does not reach to the bottom.

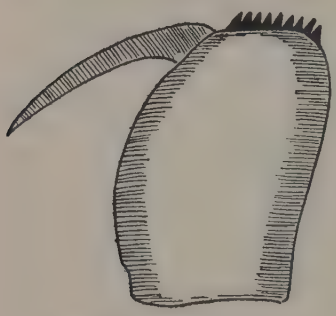


Fig. 101.—The Rastellus.

Several of these spiders leave their burrows open. This is the rule in the genus *Leptopelma*, where the lining is extended above the ground, in the form of a hollow cone of clean white silk. One species, *Cyrtauchenius inops*, surmounts the burrow with a small rampart of earth; others, of the genera *Phaeoclita* and *Celidotopus*, roughly protect it by a few leaves dragged together and attached to the silk.

But the normal burrow is closed by a door, continuous across a short hinge with the silk lining. When, as is usually the case, the burrow is dug in a bank, the hinge is placed at the highest point of the door, so that the latter shuts by its own weight.

The two different types of door are known as the cork

door and the wafer door. The cork door is hard and thick, with bevelled edges which fit closely into the mouth of the tube. It is made of alternate layers of silk and earth. The spider usually covers the outer surface, consisting of earth, with leaves, moss plants, and so on, gathered from its immediate surroundings, and these have the effect of making the closed door almost indistinguishable. Its inner surface is of smooth white silk and is nearly always pierced on the side opposite the hinge with two or more small holes. Into these the spider, when attacked, fixes its claws and holds down the door from within. The wafer door is less perfect, and consists only of a thin flap of silk overlapping the edges of the burrow. It is, as a rule, softer and less perfectly concealed than a cork door, and it has no holes inside for the spider to grasp. In some nests, however, a loose network of stout threads serves the same purpose. Both kinds of door are made of earth and silk, and Moggridge dissected a cork door into fourteen separate discs of silk.

The burrow is generally deep and cylindrical with a uniform diameter from top to bottom. In one rather interesting nest, that of *Cyrtauchenius vittatus*, the lower end is a narrow cul-de-sac, which serves as the spider's dust-bin. Into it are dropped the remains of the insects which the spider has eaten. Burrows are sometimes unbranched, but often side tubes diverge from them. These side tubes do not usually reach the surface of the ground, but in some nests they do, and provide a way of escape.

The different types of burrows are shown diagrammatically in Fig. 102. In several nests, as is shown, the branch tube is closed by an extra door of its own. These inner doors are usually stouter than the wafer doors which close the burrows, and in some cases are of an elongated oval shape. They are generally so hung that they can be used to close either the main or the side tube. One spider at least, *Nemesia eleanora*, makes an unbranched tube with a second door a little way below the first.

Particularly interesting nests are made by the spiders *Rhytidicolus structor* in Venezuela and *Cyrtauchenius artifex* in Algeria. The former is composed of three successive chambers, communicating with one another by hinged doors. The first is pear-shaped, though somewhat narrowed at its ends, the second is cylindrical and ends blindly. The third opens from the side of the second and is also pear-shaped, but rounded below. The whole is lined with soft white silk. The three doors are similar and are quite thick, fitting closely into the bevelled spaces which receive them.

The other species makes an unbranched burrow with an oval chamber at a depth of a few centimetres, in which

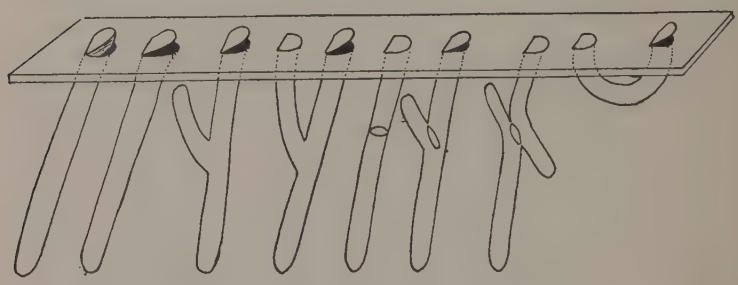


FIG. 102.—Types of trap-door nests.

the second door is hung. This door is a hemisphere of hard, fine earth coated with silk. To its inner surface is attached a tube of elastic silk. In its normal position the door exactly fits one half of the chamber, while the tube leads into the other and allows the spider to pass in and out. When the spider wishes to shut up its home, it pulls the door round, so that it rests on a small rim made to receive it and closes the burrow. In this position the tube is flattened against the side of the tube, ready to spring back and resume its ordinary position as soon as the spider releases the door.

Another member of the same genus, *Cyrtauchenius elongatus*, found in Morocco, spins a very unusual and

conspicuous nest. It has no door, the silk lining is prolonged about three inches above the surface of the ground and is enlarged in the shape of a funnel. This aerial portion is snow-white, and is a very conspicuous object among the plants to which it is attached.

All the spiders of this trap-door group are of nocturnal habits, and spend the day resting in closed burrows. Some of them mount, in the evening, to the top of the tube, raise the door with their heads till it is just ajar, allowing them to peep out. Thus they await the chance arrival of some insect upon which they quickly leap. Others, such as *Cyrtocarenum cunicularium* from the Isle of Tinos, in the Greek Archipelago, have been seen to fasten back their doors and to spin a web about six inches long and half an inch high. This web entraps low-flying insects, which the spider sucks dry, carrying away the carcase when finished. Before morning the web is removed and apparently added to the trap-door, which is then closed down for the day.

Under observation, these spiders show themselves very unwilling to leave their burrows. It is probable that in natural circumstances they very seldom do so. The young spiders for a time all share the nest with their mother, but as they grow up, they scatter and dig burrows for themselves. These are at first quite small—as Moggridge expresses it, " no larger than a crowquill "—but they seem to enlarge both burrow and door, instead of deserting them and making others.

The Migidae

The spiders of this small but interesting family are found in South Africa, Madagascar, and New Zealand. They are distinct from the burrowing spiders just described, having shorter chelicerae, not provided with teeth for excavating. The spiders, in fact, do not dig in the ground at all. They spin a short tubular nest, about two inches long, in the corky bark of certain trees, such as the " Kaffir Boom " tree, or species of oak. The bark is not dug

away; the spider makes use of natural crevices to which it fits the tube.

At one or both ends the tube is closed with a hinged door, which combines the characters of both the cork and the wafer types of the previous section. That is to say, the central part is thickened, bevelled, and fits closely into the tube, while the edge of the door is thin, and overlaps the bark outside. Both the door and the exposed parts of the tube are covered with small pieces of bark and lichen, which serve to conceal it. So perfect is the result that Pickard-Cambridge, writing of a piece of bark containing a nest, which had been sent to him from Grahamstown, said, "I had to search very minutely for ten minutes, and test every part of the pieces of bark with the point of a needle, to find out the lids of the nests."

The Atypidae

The spiders of this family have been able to establish themselves in colder regions than those inhabited by the other Mygalomorph families. They have been recognised as a separate group since Latreille, in 1802, separated the genus *Atypus* from the true Mygales, as they were then called, and all subsequent authors have maintained the distinction.

The chief structural features which distinguish the family are the possession of six spinnerets, and the position of the anal tubercle, which is some distance above the spinnerets instead of being close to them. In some species the first joints of the palpi have maxillary lobes which are similar to those of Arachnomorph spiders.

The family includes less than thirty species, found in Asia, Europe, and North and South America. Their habits are quite different from those of the Mygalomorph families which have been described above. There are two rather different types of web.

In America, the "purse-web spider," *Atypus abbottii*, occurs chiefly in the southern states. It lives in a burrow,

nearly always dug at the foot of a tree. The silk tube, which, as in other Mygalomorph nests, lines the burrow, is in this family extended outwards and by the purse-web species is carried vertically upwards against the side of the tree, as a tube about a foot long and three-quarters of an inch wide.

This tube is protected to some extent by pieces of moss, lichen, bark, and grains of sand, which the spider gathers and attaches to the outside. The final colour of the tube varies considerably from a light gray to a very dark brown, and to a great degree depends on the colour of the tree to which it is fixed. In spite of this, the tubes are not difficult to see, when one has learnt their appearance, for they are quite straight and of a uniform diameter. The tube is slightly flattened at the top, and attached so firmly to the tree that between this point and the ground it is very tightly stretched. It therefore responds to the tread of an insect by vibrating, and the spider, waiting below, rushes to the spot. It bites the insect through the web, slits the latter, and pulls the insect inside. After the prey has been sucked dry and the remains thrown away, the slit is repaired.

Only occasionally is more than one adult spider found on a tree, but six or seven tubes belonging to young ones may be found side by side

The European *Atypus*, *Atypus affinis*, which is also found in several localities in the south of England and Wales, shows a somewhat similar mode of life. The upper part of the silk tube, however, is neither raised nor attached to a tree; it merely rests along the ground. The nest is generally made in a bank, in a dry situation, and is not at all easy to distinguish. The outer side of the tube is covered with small particles of earth and sand, which, as Enock has shown, the spider obtains from the inside of the burrow, and not from the surroundings. Sometimes, however, the spider has been seen to push its fangs through the silk and drag a piece of earth into its meshes.

The British *Atypus* is an attractive little spider, about half an inch long, with a brownish abdomen and a yellow

cephalothorax, but with no pattern on either. It is a very interesting creature to keep in captivity, and to any one who is fortunate enough to find it, it well repays the trouble necessary to give it a congenial home. This is best done by Main's method, using an inverted deflagrating jar, as

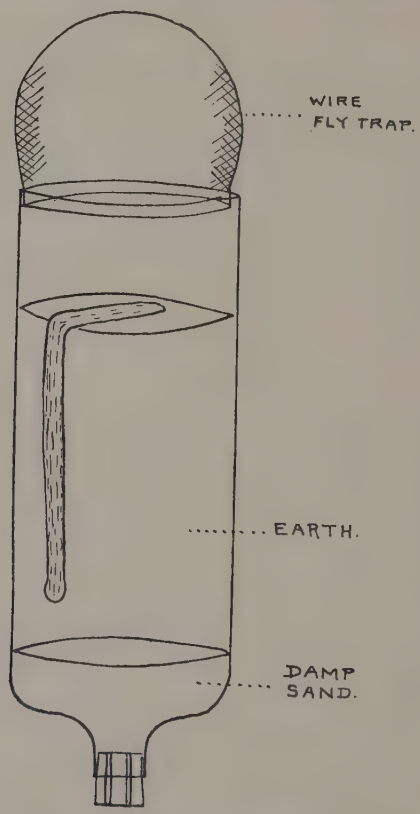


FIG. 103.—Tube of Atypus in deflagrating jar. After Main.

shown in Fig. 103 The lower end is closed by a perforated cork, which is covered by about two inches of damp sand. Clean sifted earth, slightly damp, is added above the sand, and rammed down moderately hard. During the addition of the earth a glass tube, about one-third of

an inch in diameter, is held against the glass, thus making a cylindrical hole. The spider's tube is carefully lowered into this with about two inches lying along the surface. The free end must be held in position for a day or two by a pin, stuck through it into the earth. It is necessary to avoid dryness. Therefore the corked end should be occasionally immersed in water, which rises by capillary attraction. It is not possible to keep the earth satisfactorily moist by adding water from above; in Nature the lower layers are always the source of the water supply.

In cages of this sort, all trap-door spiders will live in comfort. They will feed on earwigs, beetles, flies, and all such creatures, and do not suffer in any way from monotony or lack of exercise. The remarkable feature of their natural mode of life is that they remain constantly inside the nest, while the part of the tube which lies on the ground takes the place of the ordinary spider's web. The spider inside the tube rushes to the spot touched by a passing insect and catches it just as do the American Atypidae, which spin the purse-web. Enock discovered a curious habit which the spider shows when it is not hungry. If an insect touches the tube, the spider gives it a sharp pull, which drags a portion into the burrow. It may be imagined that this startles the intruder and prevents it from damaging the tube. The underground portion of the tube is sometimes invaded by earthworms, and it seems that the spider attacks them when they do so, for partly-eaten remains have often been found in the tube.

The male *Atypus* digs a burrow similar to that of the female, but not, as a rule, quite so deep, and he leaves it, when mature, to seek the home of a female. When he finds one, he drums on it with his palpi, an action which has already been described for other spiders. After a few moments, he tears open the tube and enters. The female then comes up and repairs the hole; she pulls the edges together with her jaws and secures them with a few threads from her spinnerets. The male and female may live together in the tube for nearly a year.

The eggs, which are about a hundred and fifty in number, are laid in the autumn, and remain in the nest during the winter. When suitable weather returns in the spring, a small hole, perhaps made by the mother, appears at the end of the tube and the young spiders squeeze themselves through it. They at once disperse and begin life on their own account. Sometimes it happens that the weather changes suddenly, before all the young spiders have dispersed. The mother then seals up the hole, and it is to be feared that she sometimes eats the young ones that remain behind.

The Bird-eating Spiders

The family Theraphosidae, to which the name bird-eating spider properly belongs, includes the largest members of all the Araneae. They are the spiders originally called *Mygale* by Walcknaer in 1802, but the name was preoccupied by a genus of mammals, founded by Cuvier in 1800. Americans usually refer to these large spiders as tarantulas, but the true tarantula is a small Lycosid of South Europe, in no way related to the present family.

Their ability to overcome the small humming birds of South America was discovered many years ago by Mme. Merian. Doubt was cast upon the accuracy of her observations and was fostered by the very foolish "experiment" of pushing a dead bird near a spider, which, probably frightened and certainly unaccustomed to any but living food, naturally took no notice of it. Bates, however, in his "Naturalist on the Amazons," gave an account of his discovery of a large spider which had captured a pair of small birds. He thus verified the original observation.

It is not to be supposed that these spiders eat birds instead of insects, but merely that many of them have the strength to overcome the tiny birds which occasionally may fall into their power. Their usual victims are insects.

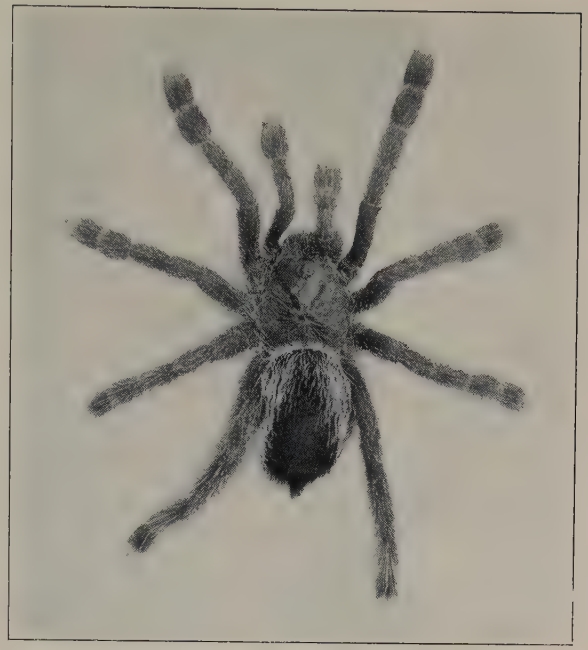
This family includes the typical hunters of the Mygalomorph sub-order. Their chelicerae have not the rake of strong teeth which characterise the burrowers, and their

PLATE XIII

A. British Trap-door Spider (*Atypus affinis*). $\times 2\frac{1}{2}$.

To face p. 296.]

[*E. A. Robins, photo.*



B. Bird-eating Spider (*Avicularia*). $\times \frac{3}{4}$.

[*H. Main, photo.*

feet are provided with conspicuous claw tufts. These claw tufts, or ungual tufts, are distinct from the scopula mentioned in Chapter II. A scopula is a group of stout spines on the lower side of the tarsus or metatarsus. A claw tuft consists of longer and less rigid setae, and is often so large that it projects beyond the actual claw and quite conceals it. In some spiders the tuft is divided so that the extremity of the leg has a bifid appearance. The bodies of these spiders are usually more " hairy " than those of the burrowing species.

The bird-eating spiders live in any chance shelter. They line the cavity with a light web, which is but seldom prolonged to any extent, and is never shaped within into the tubular retreat characteristic of so many true webs. During the day the spiders are quiescent in their retreats, and it is only towards evening that they awake and go in search of prey. They wander over the ground and also up the trunks and branches of trees, their claw tufts being well adapted for climbing—and it is here that they find the opportunity to capture small birds.

These spiders enclose their eggs in a white cocoon, which some of them carry in their jaws until the young ones hatch.

Among the many genera which the family includes there are a few which deserve special mention. One of the most interesting species is *Orphnoecus pellitus*, which lives in caves in the Philippine Islands. The spider is characterised by the smallness of its eyes, a feature which may be interpreted as the result of disuse in the course of the many generations during which its ancestors have lived in the dark. The spider is popularly credited with a poisonous bite, and it is so numerous that the natives are afraid to enter the caves on account of its presence.

The spiders of the genus *Phlogius*, although they have no rake on the chelicerae, dig deep burrows which they line with a silk tube. The burrow, however, is never closed with a trap-door, and some species extend the lining in the form of a white silk funnel, similar to that made by

Cyrtauchenius. It is very interesting to find these two genera, *Cyrtauchenius* and *Phlogius*, differing from the majority of their true allies and resembling one another as regards the type of web they spin. They thus afford a good illustration of convergent evolution.

The genus *Theraphosa* was founded for the great spider *Theraphosa leblondi*, the giant of the whole order, whose body length approaches 9 cms. This spider was described by Latreille in 1804, and the name has been several times misapplied to large spiders found in the Antilles, in Brazil, and even in Java. The true *Theraphosa leblondi* was found in Guinea, where it is a rare species with a limited distribution. The genera *Eurypelma* and *Avicularia*, the latter the original "bird-eater," are peculiar to America, and are second in size only to *Theraphosa*.

The Barychelidae and Dipluridae

The Barychelidae are an interesting family of spiders, intermediate in character between the burrowing and the hunting types. They have the two tarsal claws and long bifid ungual tufts of the hunters, combined with the rastellus, pubescent appearance and habits of the burrowers. The rake on the chelicerae is made of much finer teeth than in the Ctenizidae, and is, in fact, better described as a row of stout spines. However, the spiders dig very typical burrows lined with silk and closed by thin but rigid trap-doors, almost circular in shape. The burrow is sometimes single, with an enlarged round chamber at the bottom, sometimes branched a little way below the door, the branch having a second door of its own.

A rather unusual type of burrow is dug by *Stothis astuta* in Venezuela; it curves downwards and then turns upwards, forming a complete semicircle, and the two ends are each provided with a door (Fig. 102). Some species leave their burrows open and others close them with leaves, drawn together with threads of silk.

Other genera of this family, such as *Sason* in Ceylon,

Rianus in Penang, and the species *Sipalolasma aedificatrix*, recently discovered by Abraham in Singapore, resemble the Migidae in their habit of making their burrows in the bark of trees. These burrows are generally short and are closed by two doors. Abraham mentions that, if attacked at one door, the spider will escape at the other, but that if this door is prevented from opening, the spider will hold down the first so strongly that considerable force is needed to open it.

The marine *Idioctis littoralis*, mentioned in Chapter IX, is a member of this family, as also is the curious *Diplothele*, an Indian spider which has only the two superior spinnerets (Fig. 104).

FIG. 104.—Spinnerets of Diplothele.

The Dipluridae differ in several ways from all other members of the Mygalomorph sub-order. They have no rastellus and no ungual tufts; they have three claws of which the superior paired claws have numerous teeth; and their posterior spinnerets are long and three-jointed. In this respect they resemble the family Agelenidae, and the web they spin is of the same type. They thus provide another striking example of parallel evolution, having produced, from the beginnings of a lined retreat, exactly the same web as have certain of the Arachnomorphae, whose webs, we believe, arose from a similar origin. They never live underground; their large webs, which are of light transparent silk, ending in a tube which is open behind to permit escape, are found both among rocks and between the roots of trees. The family is widely represented in Central and South America, in Central Asia, reaching the Eastern Mediterranean, in Madagascar, Australia, and in New Zealand.

CHAPTER XV

THE EVOLUTION OF SPIDERS

In an early chapter of this book a longish passage was devoted to a discussion of the method by which scientific progress is made. The length of that passage was justified both by its own importance and by its application to the present chapter; for here it is to be seen that the advance of the biological sciences does not differ in character from the advance of the physical sciences. The same methods are used in both.

The Evolution Theory

The nature of a scientific hypothesis has already been indicated. It is a tentative formulation, based on the recorded facts of the science, with the intention of so expressing the relationship between them as to render them intelligible. A hypothesis is an attempt at an explanation, born of the innate desire of the human mind to rationalise the data set before it, that perchance it may find an answer to man's eternal "Why?"

The test of a good hypothesis is its utility, its living spirit. If it assimilates new facts, points the way to new discoveries and corrects past errors, it is justifying itself. It is a good hypothesis. But it is not necessarily true. Many a useful hypothesis is a conscious fiction, perhaps little more than a vague analogy; yet it is clear that even conscious fiction has its part to play in the advancement of learning.

When, however, a hypothesis retains its value for many

years, and especially when it maintains it without additions, modifications, or loss of fertility, then man becomes more and more inclined to believe in its truth, to trust it unquestioningly, to teach it dogmatically to the next generation.

If this scientific use of hypothesis is understood, the theory of Organic Evolution is less likely to be misunderstood. It is the underlying hypothesis of all biological progress. All the facts of biology demonstrate one supremely important truth, that of the adaptation of the organism to its environment. The shape, size, and colour of an animal, its habits, its internal structure, its physiological balance or correlation of parts, all are such that the individual is able successfully to carry out the competitive activities which constitute its life. This major fact of adaptation must find first place in all biological theory. The geographical distribution must also be kept in mind. Some creatures are numerous, others rare; some range the world, others are found only within confined limits; some are independent, others parasitic.

The history of biology has seen two hypotheses which aim at formulating these facts of adaptation and distribution. There is the hypothesis of Special Creation and the hypothesis of Evolution, or Descent with Modification. The first theory cannot pretend to be a scientific account of the facts, and is rather an interpretation than a description. The second theory, the Evolution theory, is the only scientific attempt to describe how living creatures have come to be what they are.

It is outside our present scope to discuss the rivalry between these theories. At present all biologists are agreed that evolution of animal and plant life has indeed occurred and is still occurring. The problem which remains a matter of uncertainty and discussion is the method by which this evolution has taken place. The contributions to this aspect of biology which Lamarck, Darwin, Weismann, de Vries, and Mendel have made will not be appraised here, but it may perhaps be pointed out that their several theories

are not necessarily in conflict with one another. Because Mutation may make good its claim to be considered as a potent factor in evolution, it is not necessary to deny the truth of Natural Selection or of the effects of use and disuse. Evolution is a mighty progressive force in the world of living organisms, certain to make use of every available channel for achieving results. It is not to be limited to a formula and confined to acting by one method only.

Spiders as Evidence of Evolution

Our present purpose is to try to show that the spider may claim to provide support for what may be termed the Neo-Lamarckian school. Kammerer's important experiments on toads and salamanders provide the facts on which these ideas are based. Kammerer showed that changes in the colour of the surroundings, as from black to yellow, provoked corresponding changes in the body colour of *Salamandra atra* and *Salamandra maculosa*, changes which were sufficiently deep-seated to be represented in the next generation. In the same way, the change from a moist to a dry environment altered not only the number of young produced at a birth, but also the stage of development at which they were born.

It is this response of one generation to a new environment, and the acquisition of new habits of life which shall be impressed on the next generation, that spiders also show when the history of their race is studied. For the purpose of tracing the working of an evolutionary tendency, spiders are particularly suitable, for various reasons.

In the first place, the order of spiders, like the order of birds, possesses a large number of species, approaching twenty thousand, within the limits of a comparatively small range of structural diversity. This means that there is a dense population within narrow limits, and in consequence there is a better chance of our being able to follow the course which Evolution has taken. There is less likelihood

of breaks in the chain, with the search for missing links and the suggestion of imaginary intermediate forms which such gaps produce. Yet, although the structure is uniform the habits are widely different, as the whole of this book has shown. Now that the importance of habit as a factor in evolution has been realised, spiders deserve serious consideration from phylogenists, who in the past have been wont to base their hypotheses on the facts of morphology alone. Yet more than thirty years ago F. Pickard-Cambridge wrote, " Now it would seem that either habit produces variation in structure, or slight variations in structure give rise at length to peculiar habits, or they both arise simultaneously with mutual influence, and whether the habit has resulted from a modification of the structure, or the structure from the habit, or each acted and reacted upon the other, certain it is that we cannot now (in the case of spiders at all events) well conceive of, or deal with the one apart from the other, and that, therefore, they must both perforce be taken into consideration in schemes of classification, a conclusion to which Dr. Thorell has long since come."

The correlation between habits and structure is in spiders most conspicuous in the legs and spinnerets. The question as to whether habit or structure made the first appearance still remains, but a growing body of evidence seems to point to the habit as the initiator of change. For example, Elliot Smith, in describing the evolution of the human brain, has shown how change of habit and change of structure have gone hand in hand ; he has stated that, in this instance at least, the only tenable hypothesis is that the change of habit had come first and that the change of structure had followed.

Another feature of the order of spiders is that there is no doubt about the starting point. The primitive nature of the Liphistiidae has already been fully described, and with the help of the suggestions as to the nature of the primaeval spiders which have been made in earlier chapters, it is possible to compose a satisfying description of the

hypothetical creature which may be regarded as the ancestor of all spiders.

Ancestral Spiders

Our Archearanead (Fig. 105) was therefore probably a hunter of insect prey. It had eight eyes quite close together and its cephalothorax was joined to its abdomen by a broader waist than that of recent spiders. This waist was the first of twelve visible segments of which the abdomen was composed. Below, the abdomen had four lung-books on the second and third segments, and eight spinnerets on the fourth and fifth. Its first pair of legs was the shortest, and each tarsus had three claws, unprovided with teeth. Its home was at first a chance cavity, and the appearance inside this of the tubular silk lining,

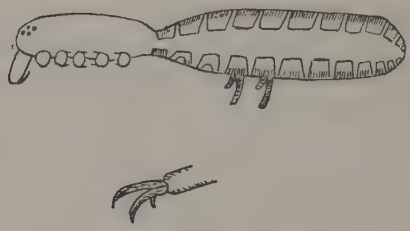


Fig. 105.—The Archearanead. A hypothetical ancestral spider.

diverging at the mouth, has already been described in Chapter VII.

From this beginning evolution has proceeded on three different lines, expressed in the three sub-orders of our modern classification.

The first and shortest of these ends in the Liphistiidae, which differ from the Archearanead in having a narrow waist and one or two teeth on their tarsal claws. They close their nests with a trap-door. In the other two lines, the posterior abdominal segments have been lost and only the anal tubercle remains to recall their existence. The spinnerets therefore seem to have shifted backwards, but in reality they occupy their original situations, modified

only by an increase in the length of the third segment, which has occurred in some species.

The second line is occupied by our present order of Mygalomorphae, described in the last chapter. They more closely resemble the Liphistiomorphae than the Arachnomorphae, but very early in their racial history diverged into two groups. These were the hunters and the burrowers already described, and in this sub-order in particular it is difficult to suggest any alternative to the idea that these changes of habit preceded changes of structure.

The third line led to the type of spider dominant throughout the world to-day, the sub-order Arachnomorphae. In tracing the evolution of the numerous forms which this sub-order contains, we make use of the significant fact that there exists a web precisely similar to that of the modern Liphistiidae, with the exception that it has no trap-door. This is the web of *Segestria*, described in Chapter VII. The Dysderidae, the family to which this genus belongs, are divisible into two sub-families, Dysderinae and Segestriinae, of which the former are the more active, the latter more sedentary. These have accordingly retained a type of nest which comes very near to that of the ancestral spider. For some reason they have never closed the tube with a trap-door, and this may be because the radiating threads gave sufficient warning of the approach of intruders, or because the spiders adopted the habit of turning the third legs forwards, thus having six limbs available for attack and defence in the mouth of the tube.

Anatomically the nearest allies to the Dysderidae are the Oonopidae. Some of the spiders of this family carry a dorsal shield on the abdomen which cannot fail to recall the segmented plates which characterise the Liphistiidae. It may one day be possible for embryological research to prove that this shield of the Oonopidae is homologous with the plates of the Liphistiidae, but that the former, in persisting, has lost its segmental character.

If these views be accepted, these families and their

allies will form the most direct line from the primitive ancestor and must be considered as the founders of the Arachnomorph sub-order. In modern classification, there are seven families in this early group, which afford material for more detailed consideration.

Methods of Respiration

In the first place, it is interesting, and perhaps not without significance, to notice that three families, Dysderidae, Oonopidae, and Caponiidae include species that have only six eyes.

There is also a most significant diversity in the respiratory organs possessed by these families. It has already been said that all Liphistiidae and Mygalomorphae have two pairs of lung-books, while the vast majority of Arachnomorphae have a single pair of lung-books and one median tracheal aperture. However, five families, all included in the present group, are exceptional. The Hypochilidae have two pairs of lung-books, the Dysderidae and Oonopidae have a pair of lung-books and a pair of tracheal apertures, while the Caponiidae and Telemidae have no lungs, but two pairs of tracheal apertures. Thus there seems to be, among the spiders of this stage in evolutionary history, an instability of the respiratory system, with the result that different methods have been produced and some of the results of each experiment have survived.

The Hypochilidae, because of their four lung-books, were something of a problem when the number of lungs was made the distinguishing feature between the trap-door and other spiders. They have been placed in both sub-orders by different authorities, and some reasons for uncertainty still exist. A study of their circulatory system or of their coxal glands, would, as Petrunkevitch has pointed out, probably settle the question without doubt, but no such study has yet been made. If they are placed among the Mygalomorphae, they will be quite isolated there, for they have a cribellum and calamistrum, which no Mygalo-

morph spider possesses. They have more affinities with Arachnomorphae, and the existence of diverse types of respiratory systems in this sub-group shows that these organs cannot be regarded as of great systematic value. Their position among the Arachnomorphae may be justified if it be merely admitted that they alone have retained the primitive means of breathing. The genus *Nebalia* occupies a very similar position among the Crustacea, and is placed among the higher Malacostraca with the same reservations.

The tracheal system of the other families has replaced the second pair of lung-books, opening at first at a pair of spiracles. Later these joined. A transitional stage is seen in the Filistatidae, where the groove uniting the two tracheal openings is already shorter and deeper.

This family is another which is in some ways a puzzle. They are cribellate spiders which live in a web very similar to that of our common *Amaurobius*. Their coxal gland system was studied by Buxton and found to be of the simplified type, like that possessed by the Epeiridae. Buxton therefore suggests that the true position of this family is near the top of the spider kingdom, and that they have descended to protected situations nearer the ground for spinning their webs. In favour of this idea there is the fact that there is a family of spiders, the Uloboridae, closely related to the Epeiridae, and occupying, as will be seen presently, some such situation as that from which the Filistatidae might be supposed to have come. If the Filistatidae are the descendants of the Uloboridae, they form an exact parallel to that section of the Linyphiidae which, as already noted in Chapter VII, took the sheet-web back to the shelter of crevices in the ground. Against the theory there is the fact that the external structure of the Filistatidae does not suggest an alliance with the Uloboridae or with the Epeiridae. This is especially true of the palpal organ of the males, which is of a very primitive type, and points to their nearer relationship to the Dysderidae and other families of the lowest group. However, their mouth parts and chelicerae are very similar to those of the Sicariidae,

and their courtship is also allied to that of the higher families.

The family has always been a puzzle, ever since Walckenaer and Koch classed it with the Mygalomorphae. There are good arguments in favour of both positions and as yet no apparent way of reconciling the two sets of opposing views.

The Cribellum

The significance of the supernumerary spinning organ or cribellum and the accompanying comb or calamistrum on the metatarsus has long been discussed. Many spiders of similar structure and habits are readily distinguished by the presence or absence of these organs, and Simon used this character for splitting his Araneae verae (a division corresponding to the Arachnomorphae) into two sections, Cribellatae and Ecribellatae. If our classifications are to deserve the adjective "natural," this is equivalent to implying that these two sections represent different routes in the history of the spider race, in which the cribellum made a very early appearance. The numerous instances of resemblance between cribellate and ecribellate genera would then have to be ascribed to a rather astonishing amount of "convergence." Petrunkevitch, who goes into the matter in great detail, has come to the conclusion that the cribellum is indeed an ancestral possession. From the first cribellate spiders, some, also cribellate, have arisen, but in others the cribellum has become the colulus, and an ecribellate spider has thus resulted. And, of course, such spiders have given rise to other ecribellate forms.

It is thus impossible to look upon the presence or absence of this organ as splitting all spiders into two fundamentally separate groups. It might even be justifiable in some cases to unite both cribellate and ecribellate genera into the same family. Whether or not this is to be done is of small importance, and is largely a question of individual opinion. Probably it is of greater practical convenience to separate them.

The Tarsal Claws

The remaining families of spiders, whether cribellate or not, which all breathe by two lung-books and a single tracheal spiracle, divide themselves broadly into those with three tarsal claws and those with two. This recalls the similar division of the Mygalomorphae and depends on the same difference in the mode of life. Like that division, too, it is not complete, for there are a few families, such as the Zodariidae and Palpimanidae, which include both two and three-clawed genera. On the whole, however, it is a convenient and probably a natural separation.

The two-clawed group consists of one fossil family, the Parattidae, and fourteen recent ones, with some differences in their general modes of life. The most important families, the numerous Clubionidae and Drassidae, contain the spiders that merely wander, usually at night, without great power of speed or conspicuous ability to leap and so prey upon what they may chance to encounter. Indeed, among the Clubioniidae there are genera, such as *Corinna*, which spin the primitive form of diverging tube-web.

Fig. 106.—Tarsus of Clubiona spiderling, showing transitory third claw. From a photomicrograph by R. W. Barney.

The two other chief modes of life in this division are obvious elaborations of simple wandering. The crab-spiders, or the family Thomisidae, often hidden by the protective colourings which have been already described, lie in wait for their prey and leap, perhaps sideways, upon it. The large Sparasside are flattened crab-like spiders, which generally conceal themselves in narrow crevices. The jumping-spiders or Salticidae have developed the habit of leaping upon their prey instead of chasing it, a method which, if one may judge from the multitude of species and world-wide distribution of this family, has certainly been very successful.

The most interesting feature about the two-clawed spiders is that on the tarsi of the spiderling in the cocoon the full complement of three claws is present. Fig. 106, which illustrates this, is drawn from a photomicrograph, originally published in *Nature* in 1926, of the leg of a spiderling of the species *Clubiona interjecta*. The tiny median claw, plainly visible between the paired claws, is lost very early in the spider's life, but its transient appearance shows that the possession of three claws is the ancestral condition.

House-Spiders and Wolf-Spiders

By far the greater number of living spiders possess three claws throughout their lives, and form a group divisible into four sections.

The lowest of these is certainly the group of seven families which includes the Agelenidae and the cribellate Amaurobiidae. The common bluish webs of the latter are undoubtedly the cribellate analogue of the primitive diverging tube. The extension by the Agelenidae of the lower edge of the tube mouth into a hammock-like sheet has already been described. The Psechridae are obviously allied to the Amaurobiidae and the long spinnerets of the Hersiliidae are among the features which relate this family to the Agelenidae.

Secondly, there is a group of nine families which are best regarded as a specialised offshoot from the group just considered. Like the two-clawed division, most of these spiders have taken to hunting their prey, which they overcome by sheer speed. The wolf-spiders, Lycosidae, and the Pisauridae are the best known of these families. The latter are actually the more primitive, but the resemblance between the Lycosidae and the Agelenidae are very striking. The most significant from the point of view of this chapter is the fact that some genera of the Lycosidae, such as *Hippasa*, spin large sheet-webs of the same form as the webs of the Agelenidae. It was indeed the form of these

webs which first suggested to Simon that the Lycosidae and the Agelenidae might prove on examination to be related—a relationship which, as he says, in speaking of the advantage he gained from foreign travel, "nous aurait sans doute tourjours échappé si nous avions restreint nos recherches à la faune de France."

Of the other families in this group, the Senoculidae form an American family obviously allied to the Pisauridae, as are the Oxyopidae to the Lycosidae. The Palpimanidae and the Zodariidae are rather primitive and in some ways resemble the Drassidae, but some of their species have three tarsal claws. The exact position of the last family, the Eresidae, has always been something of a puzzle, for they show a superficial resemblance to the Salticidae. It is probable that this is due to convergence and their true position is to be found among the hunting-spiders.

Web-spinning Spiders

Our hypothesis concerning the origin of the last two groups, as the sheet-web was modified on being taken into arboreal situations, has already been stated in Chapter VII.

The group which contains the sheet-webs of the Linyphiidae and the simple tangles of the Theridiidae consists of five families. The Pholcidae have from the first been recognised as closely allied to the Theridiidae, and the Archaeidae are similarly related to the Linyphiidae. The last family, the Dictynidae, are a cribellate group, which may reasonably be regarded as the arboreal descendants of the Amaurobiidae. Indeed, it is only lately that Petrunkevitch has separated these two families, which were previously united.

The last group of all is much the hardest to place satisfactorily. It contains four families, the Epeiridae, Mimetidae, Dinopidae, and Uloboridae, and it seems impossible to derive it directly from any family in the Agelenidae group. It may be represented as an early offshoot of the third or Linyphiidae group, with whose

families its own are closely parallel. There are obvious similarities between the Dictynidae and the Uloboridae, two cribellate families which both have claims to a genus

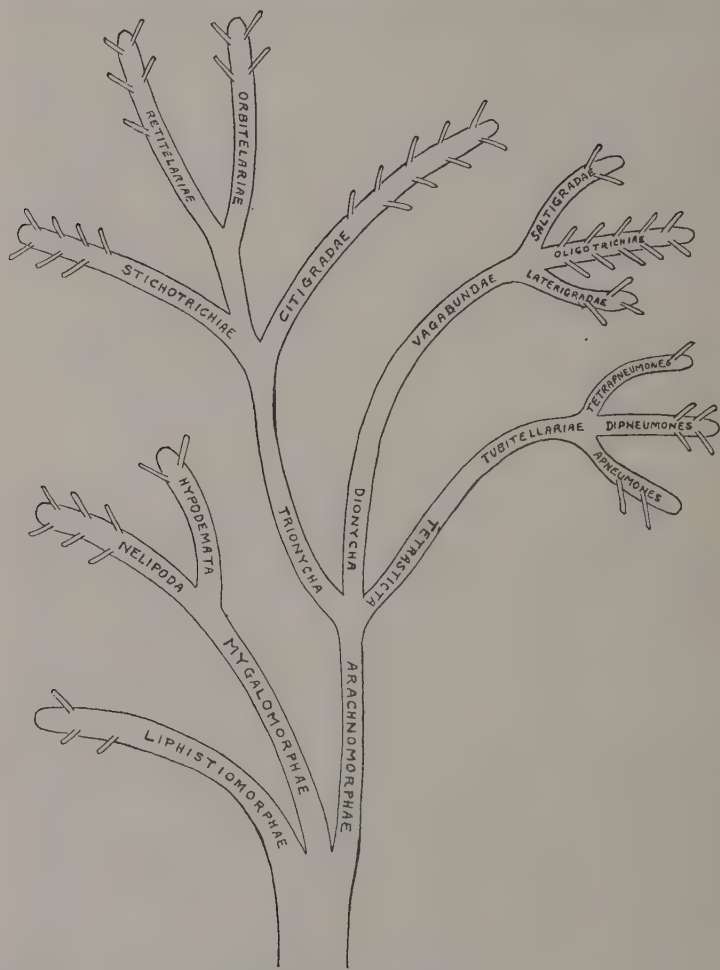


FIG. 107.—The Spiders' Genealogical Tree.

Æbutina. The Mimetidae recall the Theridiidae in several respects, including the form of their webs, while the relation between the Epeiridae and the Linyphiidae, the

supreme families of the two groups, is so close that Simon united them into one huge family, Argiopidae.

These ideas are summarised by the diagrammatic Evolutionary Tree in Fig. 107.

All the foregoing derivation of one set of families of spiders from one another is, like the early part of Chapter VII, of very recent date and includes the spider's chief claim to consideration as an animal able to make serious contribution to the theory of biology. The first suggestion of an evolutionary relationship between the different families was made by Thorell in 1869. In a plate in his book, *On European Spiders*, he gives a diagrammatic representation of the tracks of evolutionary progress, in which he makes the Tubitellariae the lowest group, containing the families Drassidae, Dysderidae, Agelenidae, and others with the "Liphistioidae" as one of several offshoots therefrom. It seems, however, quite clear that the Liphistiomorphae must be the starting point.

In the authoritative *Histoire Naturelle des Araignées*, Simon puts forward the views both of himself and others as to the relations of each family in turn. If one takes stock of all these statements, one gets the impression of a direct linear ascent from the lowest to the highest forms, with many convenient intermediates, but with plenty of room for divergence of opinion.

The most important contributions to the subject are two recent papers by Petrunkevitch. The former, *On Families of Spiders*, appeared in 1923 and was generally recognised as one of the most striking contributions to the systematic study of any group of animals that has ever been seen. The latter, *Systema Aranearum*, an invaluable monograph of nearly three hundred pages, appeared in January, 1928, and brings together, for the first time in the history of arachnology, the whole of the 2,144 genera established to date.

The Classification of Spiders

Zoologists regard the subject of classification from at least three different points of view. There are some who affect to despise taxonomy as the Cinderella of natural history, and there are those who, almost grudgingly, recognise that animals must be grouped into orders, families, and genera, but who sternly repress any attempt to push the division to finer intermediate stages. Finally, there are the few who realise that our classificatory schemes not only summarise the results of the labours of embryologists, morphologists, and others, but that, when reasonably complete, they will tell the whole history of animal life, recording age-long experiment, success, and failure in the ever-present problems of self-preservation and race-propagation. To the last class taxonomy becomes a valuable aid in the study of zoology, for, instead of remaining bound by convention, it confers its greatest benefits by becoming a live branch of the science, elastic where elasticity is desirable, and not bound down to arbitrary and probably artificial limitations. The classification of spiders, in particular, responds to such a mode of treatment.

It is not so very long since the subject of spider classification was in a state of chaos and confusion. The difficulties with which earlier workers had to contend were due in part to their ignorance of the fauna of many distant quarters of the earth, so that fresh discoveries failed to find a place in their schemes. Partly because of this, many systematists went to work on fundamentally the wrong lines, endeavouring to arrange the order in a few large divisions, instead of a greater number of almost equivalent groups. Thus C. A. Walckenaer, in 1805, divided spiders into "les Theraphoses," and "les Araignées," which were further split into "les Binoculées," "les Senoculées," and "les Octoculées." P. A. Latreille, in 1809, adopted two sub-orders—"Quadripumonaires" and "Bipumonaires," —but sixteen years later produced a new scheme of division into tribes, based on the habits of their members. There

were the Orbitelariae, Retitelariae, Citigradae, Laterigradae, Territelariae, and Saltigradae. The method was followed by many naturalists, by some quite closely—as by Menge in his "Preussische Spinnen"—by others with slight modifications, such as the interpolation of the groups Vagabundae and Sedentariae. In fact, it had more to recommend it than some of the systems which followed.

Daylight began to break over the families of spiders when the amazing industry and genius of the late Eugene Simon produced the second edition of the *Histoire Naturelle des Araignées* between 1892 and 1903. It cannot, however, be said that Simon's grouping of his forty-one families was altogether fortunate. His major divisions were as follows :—

Sub-order. Araneae theraphosae. (3 families.)
Sub-order. Araneae verae.
  Section Cribellatae. (8 families.)
  Section Ecribellatae.
    Sub-section Haplogynae. (6 families.)
    Sub-section Entelegynae. (24 families.)

The validity of the two sections has already been criticised. The last two sub-sections depend on whether the epigyne of the female is medially divided into right and left halves, or not. This is not a character of a very fundamental nature, and the six families of the Haplogynae do not form the whole of a natural group in the scheme outlined below.

It is not difficult to see why a method of sub-division such as this should have recommended itself to one in Simon's position. It must be remembered that he did all the pioneer work of modern arachnology ; that he collected spiders himself in every part of the world, and that later, as the unchallenged and unchallengeable head of the devotees of these creatures, he received specimens in almost overwhelming numbers. At the time of his death in 1924 his collection contained some twenty-six thousand tubes with about a quarter of a million specimens.

The task of surveying such a multitude might well have

dismayed a lesser man, and it seems only reasonable to suppose that the system he adopted was favoured because of its practical advantages in classifying specimens. It is easy to see if a spider has a cribellum or not, or whether its epigyne is divided or not. At the time, this was of greater value than the establishment of a wholly natural scheme. Even now, an artificial rather than a natural " key " is the most convenient method to use, when it is necessary to determine the family of a given spider.

The aim of taxonomists, however, is to give a natural classification, in which the relation between the different groups shall be the same as their actual and historical origins. For instance, there are, as we have seen, three distinct groups of hunting-spiders and at least five distinct groups of web-spinners among the Arachnomorphae alone. All these represent different lines of development of the spider race, and, as our classification stands at present, exist as nameless and all but unrecognised stages intermediate between the sub-order and the family. It is, of course, possible to leave them unnamed, and many will wish to do so, partly from innate conservatism, partly from an apparent horror of admitting any new division between family and sub-order. But if we do so, our scheme of classification is at once becoming stereotyped, ceasing to be natural, ceasing to express racial history, and losing its most valuable function of summarising existent knowledge. It becomes a dead index, in which alphabetical order would be as good as, or better than, any other.

The possible alternative is, of course, to make the family a larger body, including a greater number of genera. There are many to whom such a course would appeal—those who possess an " inclusive " type of mind, and who delight in obliterating boundaries wherever " intermediate forms " make it possible. In this way the Insecta and Myriapoda have become the Antennata ; the Annelida and Arthropoda have become the Appendiculata, and so on. An obvious criticism of this process is that, carried by increase of knowledge to its logical conclusion, the whole

animal kingdom becomes one phylum (or one genus), and taxonomy has disappeared. This is perhaps an idealist absurdity; the real drawback is a practical one—the unwieldy character of the groups it produces.

It has to be realised that there is not, in the present state of our knowledge, any stage in the separation of organisms where, by fixed rule, one family or genus ends and the next begins. Our classifications are made to be of use to us, and at present workers have little hesitation in splitting a family or genus into several parts when the number of contained genera or species exceeds a useful limit. This is the antithesis of the inclusive mind—it is a mind which delights in finer and finer subdivisions, in more and more precise analysis. It has this obvious justification, that its schemes become of increasing utility without losing their claims to be considered natural, while at the same time they avoid that appearance of a linear ascent through all units of the series, which is just the way by which evolution has not travelled.

For the Evolutionary Power was never an Urge which at any time decreed, "Here and now shall a new family (or genus) be created." Our division into families and genera are devices of our own subsequent invention and for our own convenience. We have to try to make them as natural, as true, as possible, and not to try to force the facts of nature into our schemes. There is always the risk of our treating our classifications with more reverence than they deserve, for families and genera, and perhaps species too, are inventions of man and not creations of Nature.

The present chapter ends with a classification which differs from that of Petrunkevitch only in emphasising the varied direction in which Evolution has proceeded. Thus each separate experiment of the past is represented by a named group of families. This has necessitated the introduction of stages between the sub-order and family, which I have called divisions, tribes, and grades. Each of these is named, and as far as possible, the names suggested

for them are resurrections of the proposals of other writers, which would otherwise be forgotten. These are not now used with necessarily the same significance as that which they originally possessed, but it seems more reasonable to use them than to invent an entirely new series of names for expressing very much the same ideas.

Order ARANEAE

I. Sub-order LIPHISTIOMORPHAE

1. Family Liphistiidae . . . (2)
2. Family Arthrolycosidae . . (1)
3. Family Arthromygalidae . . (1)

II. Sub-order MYGALOMORPHAE

Tribe NELIPODA

4. Family Ctenizidae . . . (3)
5. Family Atypidae . . . (1)
6. Family Migidae . . . . (3)
7. Family Dipluridae . . . (5)
8. Family Paratropididae . . . (1)
9. Family Pycnothelidae . . . (1)

Tribe HYPODEMATA

10. Family Barychelidae . . . (4)
11. Family Theraphosidae . . (7)

III. Sub-order ARACHNOMORPHAE

A. Division *TETRASTICTA*

Tribe TUBITELLARIAE

Grade TETRAPNEUMONES

12. Family Hypochilidae . . . (1)

Grade Dipneumones

13. Family Filistatidae . . . (1)
14. Family Dysderidae . . . (2)
15. Family Oonopidae . . . (2)
16. Family Hadrotarsidae . . . (1)

Grade Apneumones

17. Family Telemidae . . . (1)
18. Family Caponiidae . . . (1)

B. Division *DIONYCHA*

Tribe VAGABUNDAE

Grade Oligotrichiae

19. Family Zoropsidae . . . (1)
20. Family Acanthoctenidae . . (1)
21. Family Ctenidae . . . (3)
22. Family Drassidae . . . (4)
23. Family Ammoxenidae . . . (1)
24. Family Prodidomidae . . . (2)
25. Family Homalonychidae . . (1)
26. Family Selenopidae . . . (1)
27. Family Clubionidae . . . (5)
28. Family Platoridae . . . (1)

Grade Laterigradae

29. Family Thomisidae . . . (6)
30. Family Aphanthochilidae . . (1)
31. Family Sparassidae . . . (7)

Grade Saltigradae

32. Family Salticidae . . . (23)
33. Family Parattidae . . . (1)

C. Division *TRIONYCHA*

Tribe STICHOTRICHIAE

34. Family Œcobiidae . . . (1)
35. Family Urocteidae . . . (1)
36. Family Psechridae . . . (3)
37. Family Tengellidae . . . (2)
38. Family Amaurobiidae . . . (1)
39. Family Agelenidae . . . (4)
40. Family Hersiliidae . . . (1)

Tribe CITIGRADAE

41. Family Palpimanidae . . . (3)
42. Family Zodariidae . . . (6)
43. Family Eresidae . . . (2)
44. Family Pisauridae . . . (3)
45. Family Lycosidae . . . (5)
46. Family Senoculidae . . . (1)
47. Family Oxyopidae . . . (1)
48. Family Leptonetidae . . . (2)
49. Family Sicariidae . . . (7)

Tribe RETITELARIAE

50. Family Dictynidae . . . (2)
51. Family Theridiidae . . . (11)
52. Family Pholcidae . . . (6)
53. Family Linyphiidae . . . (6)
54. Family Archaeidae . . . (2)

Tribe ORBITELARIAE

55. Family Uloboridae . . . (3)
56. Family Dinopidae . . . (1)
57. Family Mimetidae . . . (1)
58. Family Epeiridae . . . (7)

NOTE.—The numbers in parentheses after each family refers to the number of sub-families into which the family is divided by Petrunkevitch in his latest work. The number of genera is as yet too uncertain to be usefully included.

CHAPTER XVI

SOME OTHER ARACHNIDA

BESIDES spiders, there are other orders of Arachnida, whose more interesting features may be considered in a final chapter. Thus will the arachnid corner of the animal kingdom be surveyed, and a comparison made between spiders and their nearest allies.

THE KING-CRAB

The king-crabs form a genus, formerly known as *Limulus*, of primitive Arachnida of an extraordinary type, differing in several ways from all other members of the Class. They are marine creatures, living in waters less than ten fathoms deep on the Atlantic coast of America and in a few localities near Japan, Malaysia, and India. About half a dozen living species are known.

In appearance the king-crab (Fig. 108) may be roughly compared to a semicircle linked to a hexagon. The semicircle is the outline of the sloping carapace which is rounded in front. The abdomen is a broad hexagon, its anterior margin fitting into a re-entrant behind the cephalothorax, its posterior margin edged with spines and bearing in the middle a long unjointed spine-like telson. The colour varies from dark green to black, and the creature has a clean-looking, burnished appearance. The only other feature visible from above are the eyes, of which there are two pairs, one median, the other lateral.

The lower aspect of the king-crab is a deep hollow, in

which the appendages lie. Of these there are seven pairs belonging to the prosoma.

The chelicerae, which mark the third segment of the animal's body, lie just in front of the mouth. They are very short and consist of three joints only. The third joint is chelate, ending in a delicate pair of points like those

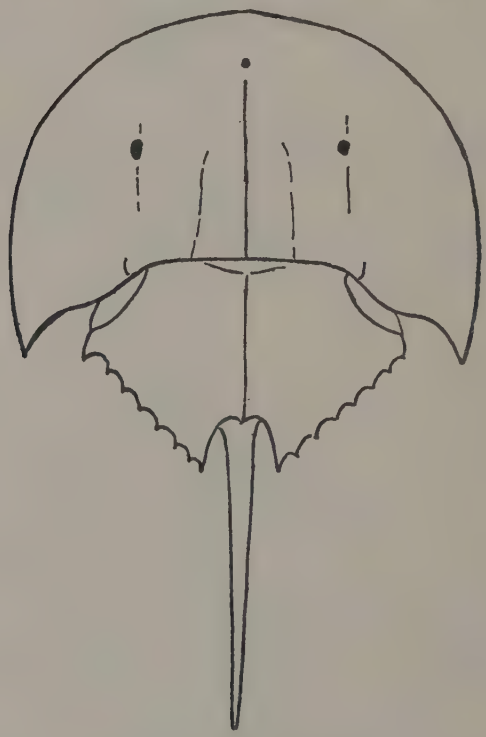


FIG. 108.—The King-crab.

of fine forceps. The pedipalpi have six joints. In the females of some species the last joint is chelate, in others it ends only in a claw. In the mature males the pedipalpi end always in a claw, and the organ is thicker and heavier than in the female. The legs are also composed of six joints. The first three pairs are chelate. The fourth pair end in a number of fan-like plates, which can be separated

or brought close together. These are used in burrowing. The last pair of appendages on the prosoma are the chilaria.

The coxal joints of the pedipalpi and of all the legs have inwardly directed processes covered with spines and furnished with crushing teeth. They assist in masticating the food before it enters the mouth.

The appendage of the first abdominal segment is the median genital operculum, through which the female deposits the eggs. The next five segments carry paired gill-books (Fig. 109). These respiratory organs are very different from anything possessed by the land Arachnida. The gill-book itself is borne on the hind surface of the expodite or outer branch of the appendage. It consists of a hundred and fifty to two hundred leaves within each of which the blood is flowing, while the oxygenated water circulates between the leaves. In this possession of breathing organs visible from outside the body, *Limulus* resembles the extinct Eurypterida.

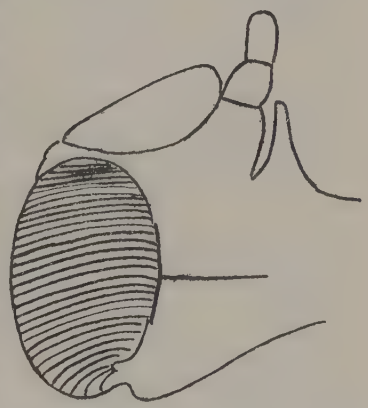


FIG. 109.—Gill-book of the King-crab. Partly after Shipley.

The king-crab spends the greater part of its life burrowing in the sand under shallow water. It is probable that in this comparatively unpopulated environment it enjoys a freedom from competition with the more active creatures, and that this has enabled it to persist in its relatively primitive form since the Silurian era. It makes its way through the mud with astonishing facility. Bending its body upwards, it urges the front edge of its carapace downwards and forwards, while the sharply-pointed spine is pressed into the mud behind. At the same time, the extensible fan-like organs which terminate the fourth pair of legs are thrust backwards, so that the lobes are opened by the

resistance of the sand, a load of which is pushed out behind the shell. This process is rapidly repeated and the clearing action is probably assisted by the fanning action of the plates bearing the gill-books, the current from which helps to wash the sand particles away.

At night the king-crab leaves the sand and swims by means of its gill-bearing appendages, helped by the spine on which it balances between the flights. Its mode of progression is therefore a kind of combination of swimming and hopping. The food of *Limulus* consists of softish molluscs and marine worms such as *Nereis*, which it encounters as it burrows in the sand. It seizes them with its chelicerae and holds them under its mouth, in such a position that they can be reached by the gnathobases of the legs. Opposing movements of the gnathobases shred the food into particles small enough to pass into the mouth.

The sexes are separate, the male, as is common among Arachnida, being smaller than the female. Fertilisation is external. The creatures come into shallow water for pairing and spawning during the months of May, June, and July, and the male grasps the hinder edge of the carapace of the female with the chelae of the second pair of legs. At intervals the couple stop for a few moments, and at each of these stopping-places, a nest of eggs may be found, buried under about two inches of sand. It thus seems probable that the female thrusts her genital plate into the sand and that at the moment that she lays the eggs, the male discharges sperms into the water. Each nest contains about a thousand eggs. Some species of king-crab do not bury their eggs but carry them about attached to their under surface in a quantity which may amount to as much as half a pint. In this condition they are valued as food for pigs and poultry.

Each egg is protected by a leathery coat. From it there emerges an interesting little creature known as the trilobite larva, because of its superficial resemblance to that fossil. The larva is very active, burrowing in the sand like its parents and also swimming freely by means of its posterior

limbs. It soon moults, when the segments of the abdomen, which had at first been free, become more closely united. The spine is absent from the larva, but makes its appearance at the first moult, and increases in size at subsequent changes of the cuticle.

Thus the king-crab grows like other arachnids. There are five or six moults in the first year of its life. In moulting, the old cuticle splits along the lower side of the front edge of the shield, and through this slit the body and legs of the animal emerge. The increase of size is rapid and an individual may reach a width of nine or ten inches. The time required to reach this size is estimated at about eight years.

Scorpions

Scorpions are the largest of the land-living Arachnida, and are interesting because their structure combines parts which indicate a state of high specialisation with parts which show a primitive nature. They are essentially dwellers in hot countries and are found widely distributed to the south of the 45th parallel of latitude in the northern hemisphere. They do not occur in New Zealand or in the Antarctic Islands.

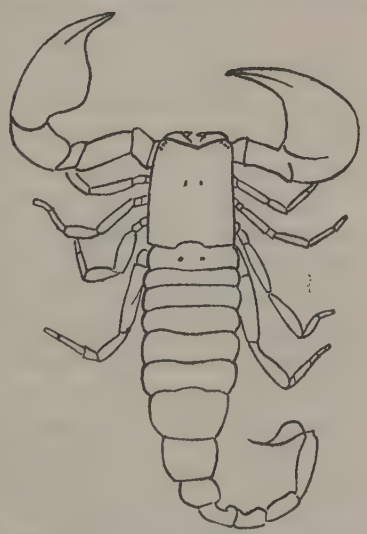


Fig. 110.—A Scorpion. From a photograph by C. Milton Adcock.

The body of the scorpion (Fig. 110) is divided into three parts, each of six segments. The first part, or prosoma, is covered above with an unsegmented carapace, bearing two median eyes and two lateral groups of from two to five eyes. All the eyes are simple, like those of spiders. Beneath the

prosoma is a very small sternum, surrounded by the six pairs of appendages. These are the same as those of the spider, namely, the chelicerae, pedipalpi, and four pairs of legs. The chelicerae are three-jointed; the third joint is articulated on the outer side of the second, forming a strong "finger" armed with teeth. The palpi are six-jointed, and also end in a movable finger-like chela. The legs are seven-jointed; the last joint terminates in a pair of stout claws, with a vestigial third claw beneath them. The teeth of the chelicerae, the last joint of the palpi, and the last three joints of the legs exhibit differences in detail which make them useful guides in classification.

The segments of the mesosoma are separate from one another, and are protected by hard tergal and sternal plates, joined at the sides by softer chitin. The second mesosomatic segment bears a pair of remarkable comb-like organs, the pectines. These seem to be special organs of touch, a sense which is highly developed in scorpions, and they are apparently in constant use determining the nature of the ground over which the scorpion is walking. Thus Pocock has seen a scorpion walk over a cockroach until the pectines came into contact with it, when it immediately backed and ate the insect.

The segments of the metasoma or abdomen are enclosed in complete chitinous rings. The last or post-anal segment has a globular base known as the vesicle and terminates in a fine curved point along which runs the poison duct. This point is usually directed downwards, but in the attitude of attack or defence the "tail" or abdomen is curved over the back and the sting points forwards.

Scorpions are nocturnal in activity and rapacious in habits. During the day they rest in hiding under logs of wood, under stones, or in holes in the sand. These holes are dug by the scorpion itself, using the second and third pairs of legs as scoops, while it supports its body on its chelicerae, abdomen, and other legs. At night they awake and hunt their prey, which consists almost entirely of insects and spiders. Their power of vision is feebly

developed and they seem to be quite deaf. There is no evidence that they possess any sense of taste. The prey is seized in the pedipalpi and torn to pieces by the chelicerae. If the victim is a formidable one, the poison-bearing sting in the tail is used to paralyse it. Like spiders, scorpions are slow eaters, and will generally spend more than an hour in eating a single beetle.

The food of scorpions seems to supply them with all the moisture that their bodies need, for they apparently never drink. They are in this respect well adapted to live in the dry sandy localities in which they are generally found, and, like other Arachnida, they can undergo prolonged fasts without fatal consequences. They are solitary animals and Warburton remarks that the only occasion on which two may be found together is when one is engaged in eating the other.

As is well known, the poison they secrete is much more virulent than that of spiders, and is instantaneously fatal to insects, spiders, and centipedes. A scorpion's own poison is, however, without effect upon itself, an interesting fact which contradicts the fable that a scorpion will commit suicide when in danger from fire. Their ferocity has been much exaggerated. They never attack without considerable provocation, and generally exhibit a much greater desire to avoid notice or to escape unostentatiously.

Their mating habits have been described by Fabre, who kept numbers of scorpions in his garden. They indulge in courtship, which is strongly reminiscent of the courtship of spiders. In a preliminary dance together their tails are entwined, and later the male takes the chelicerae of the female in his own and leads her to the neighbourhood of a suitable stone, where, without letting go, he digs a hole into which both scorpions retire. After mating the female sometimes eats the male.

All scorpions are viviparous. The newly-born young are carried on the mother's back, where they remain for a week. During this time they do not feed, and in this respect they resemble young wolf-spiders. They then

moult, after which they leave their mother and fend for themselves.

Subsequent growth takes place, as in spiders, by casting the cuticle. The size of an adult scorpion is very different in different species, some are over eight inches long, others are barely a quarter of an inch. Fabre estimates the normal length of a scorpion's life at five years.

The number of different species of scorpions known is about three hundred, and they are divided into six families :

Buthidae	Scorpionidae	Chaerilidae
Chactidae	Vejovidae	Bothriuridae

Solifugae

The Solifugae form an order of about two hundred species, interesting because of their primitive structure. There is in fact a remarkable resemblance between the general appearance of these creatures and that of the hypothetical Archearanead described in the last chapter, a resemblance which cannot be wholly due to chance. There is, however, so much difficulty in determining the relationship between the different orders of Arachnida that it would not, as yet, be justifiable to stress this resemblance further.

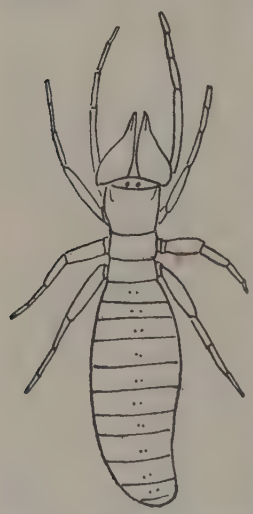


Fig. 111.—Galeodes arabs. From a photograph by C. Milton Adcock.

Solifugae are confined to hot countries. No species is found in England and in Europe they are limited to Spain, Greece, and South Russia. They abound in Africa, tropical Asia, and central America, but are absent from Australia and Madagascar.

In general appearance they are very spider-like, but they have a segmented body and no spinning organs

(Fig. 111). The cephalothorax consists of six segments, of which the first three are fused together to form a head, while the posterior three are quite separate. The abdomen consists of ten clearly defined segments. It is a little harder than the abdomen of a spider, but not nearly so hard as the body of a scorpion. The whole body and the limbs of the animal are thickly covered with hair-like setae.

The appendages of the cephalothorax are the same as those of spiders. The chelicerae, however, are greatly developed and the muscles which move them produce large " cephalic lobes " in the front of the cephalothorax. They are two-jointed chelate limbs ; the basal joint bears in the male a curious flagellum composed of modified hairs and believed to have a sensory function. The pedipalpi are leg-like and consist of six joints. The last joint is knob-like, and contains a remarkable extensible sac, believed to be an olfactory organ. There are four pairs of legs. The first have a single small claw, the others have two large claws. Sensory organs are also present on the legs. The first pair of legs is not used for walking, but is carried like the palpi and used for feeling.

A pair of large simple eyes occupies a prominent position on the cephalic lobes, and in addition one or two pairs of lateral eyes may be present.

Most Solifugae are nocturnal, but a few are lovers of sunshine ; many of them are very active, and so rapid in their movements that they are difficult to catch. Their normal diet consists of insects. In spite of the widespread belief that Solifugae are venomous, it has been shown conclusively that there are no poison glands. Bacteria, however, may of course be introduced into the wound made by the bite. The strong chelicerae can inflict such a serious wound that poison is unnecessary.

Solifugae became familiar during the War to our troops in Egypt and the near East, where *Galeodes arabs* is very common. The soldiers named them " jerrymanders," and admired them on account of their extreme ferocity. At one time the men stationed at Aboukir kept pet Solifugae

and fought them against each other, like fighting cocks. Each company had its champion, and bets were freely laid on the results of the fights.

Size is not always the decisive factor when *Galeodes* fights. Although a large one may catch a small one behind the head and not let go until the head is severed, it sometimes happens that a smaller individual seizes its opponent between its too widely-opened jaws and conquers by holding on in a position in which the big creature is quite helpless.

False-Scorpions

The false-scorpions form one of the most interesting orders of the lesser Arachnida. They are widely spread over the whole of the habitable world, being represented in small numbers even in cold countries. But the largest known species, *Garypus litoralis* of the Mediterranean, is barely a quarter of an inch long, and no British species exceeds a sixteenth of an inch in length, so that, partly because of their small size, and partly because of their retiring habits, they are comparatively little known, for they are seldom found unless specially sought.

Many of them hide under stones, under the bark of trees, among moss, and in collections of vegetable debris. A few live in houses, where they may be found in cellars and among books. The "book-scorpion" is *Cheiridium museorum*, a member of this order, and has been known since the time of Aristotle. In stables and sheds false-scorpions often occur, living in cracks in the woodwork and in neglected heaps of hay or straw. Some species are partial to heaps of manure, and one or two cling to the legs of flies as a means of dispersal. A few others live on the seashore, below high-tide mark in deep rock-crevices and under large stones.

These little creatures have a superficial resemblance to a scorpion, enhanced by their large claw-like pedipalpi (Fig. 112). The body consists of a cephalothorax and an abdomen of twelve segments. The segments are protected

by dorsal and ventral plates, but, since the plates covering the eleventh and twelfth segments are fused together, only eleven segments can be seen from above. In the same way the last four ventral plates are joined, so that only nine can be seen from below. The dorsal plates are often divided by a median line of soft membrane.

The cephalothorax has no trace of segmentation beyond a few transverse striae, present in some species. The eyes

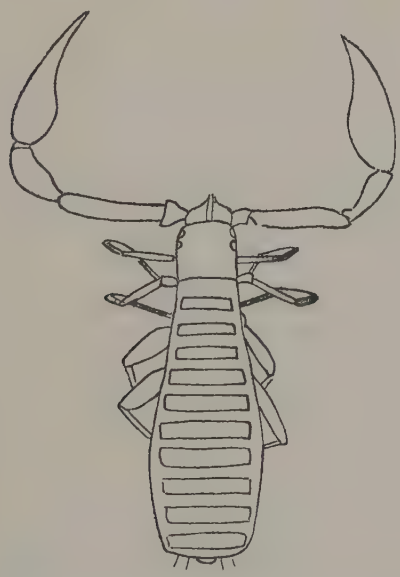


FIG. 112.—Obisium muscorum. A common British false-scorpion. After Kew.

are two or four in number, save in some species which are blind, and are placed in the usual position near the front of the cephalothorax. They are pearly white in colour and are never much raised above the level of the carapace. The ventral surface of the cephalothorax is formed by the coxal joints of the legs and palpi ; only in *Garypus* is there any trace of a sternum.

The abdomen, unlike that of the true scorpion, bears no

"tail." The chitinous plates are separated by intervals of membrane, and this membrane is very extensible. The result is that when the abdomen is distended, as it is before the female lays her eggs, the plates are some distance apart, while after the eggs have been laid, they may even overlap.

The respiratory tracheae open at the sides of the abdomen, on a level with the hind edges of the first and second segments. The first ventral plate bears the genital orifice and also a pair of other apertures from the "abdominal glands."

The appendages of the cephalothorax are the chelicerae, pedipalpi, and four pairs of legs. The chelicerae are two-jointed, and the second joint moves up and down against the prolongation of the first to form a grasping chelate organ. Near the top of the second joint there is the opening of the silk glands. False-scorpions produce a secretion similar to the silk of spiders, but use it only for nest-making.

The large pedipalpi are six-jointed, the last joint being a movable one. They form the only effective weapons of the creature. Unlike the palpi of spiders, their coxae bear no maxillary lobes; they are, however, very close together and are enlarged and flattened, so that they probably assist in mastication.

The legs are by comparison short and weak; they are composed of five to eight joints, of which the first, or coxae, are large and form a substitute for a sternum. The tarsus ends in two smooth claws, between which is a conical adhering pad or sucker.

False-scorpions are carnivorous, and their food consists of insects and mites even smaller than themselves. Thirty years ago, when Pickard-Cambridge published his monograph on the false-scorpions of Britain, very little was known of the habits of these small animals and some of the published information was erroneous. Since then, however, they have been the subject of study by With of Copenhagen and Wallis Kew in this country, with the result that our knowledge has grown both in accuracy and extent. In particular

their silk-producing organs and the nests they spin have received attention, and form one of their most interesting features.

All false-scorpions make nests of silk. In such nests they moult, and so are protected during the time of helplessness which both precedes and follows the casting of the cuticle. Female false-scorpions also make brood nests to shelter them while they are distended with eggs, and also to protect the brood pouch when laid. Finally, some species make hibernation nests in which they pass the winter.

In all species the nests, whatever be their use, are essentially similar in character. They are more or less circular in outline and rounded or globular in shape, according to the space available where they are made. They are completely enclosed and are just large enough to contain the animal in comfort without cramping. The outside is in many cases coated with small particles of earthy or vegetable debris, but from the nests of some species these are invariably absent. The nest is then glistening white, made of a material of tissue-paper-like consistency.

The silk is secreted by glands situated in the cephalothorax and passes out through ducts which open on the chelicerae. In some genera the ducts, six or ten in number, travel along a small almost transparent projecting structure known as the galea; in others there is no galea and the ducts open at a small tubercle which occupies the same place. On the tubercle there are several orifices from which the silk issues, and the presence or absence of a galea does not seem to make any difference to the way in which the creature works, or to the structure which it produces.

Wallis Kew has given the only full description of the making of nests. When a false-scorpion is about to start spinning, it may first be seen moving actively about as if seeking a suitable spot. When this is chosen, it begins by collecting a number of the small particles with which to

cover the outside, and these it arranges in a circle. The particles are picked up in the palpi, and then transferred to and carried by the chelicerae. They are built up, one upon another, by brushing the chelicerae against them and thus attaching threads of silk which hold them in place. The particles are never overspun from the outside. At first, when the circular rampart is still quite low, the animal can pick up solid particles lying near by simply reaching over; later it must climb over the wall and make longer journeys to fetch more. The silk rapidly hardens and the wall is so firm that it is not injured by the frequent climbing in and out. In this way the animal gradually encloses itself in the outer framework of its cell. When this is complete, however, its labours are by no means over. It continues to lay down silk on the inside of the walls until the paper-like consistency is attained. The threads lie in all directions, but leave no interspaces, so densely are they applied. The energy expended in this part of the work is remarkable; Wallis Kew records an instance of one false-scorpion which continued for six weeks energetically strengthening the wall of its cell.

The eggs are laid in such a cell and the story of the development of the young is a remarkable one. In the early spring about thirty eggs are laid, but they do not lose their connection with the mother. They are contained in a small egg sac which remains attached to the genital area. The abdominal glands, whose ducts open in this neighbourhood, probably have an important part to play in supplying the adhesive secretion which fixes the sac, the interior of which is still in communication with the mother's abdomen. Nutritive material is thus passed from the mother into the egg-sac throughout the period of its attachment.

The eggs themselves lie towards the sides of the sac. The embryos which develop from these eggs become true larvae, for they do not continue their development at the expense of internal yolk. Instead of that they develop a temporary stomach and a large sucking organ, with which they imbibe the fluids from the centre of the sac. These

larvae undergo a kind of metamorphosis shedding the lower half of their cuticle and entering on a stage in which the sucking organ is lost and the albuminous fluid which has been taken in is absorbed as if it were the original yolk of the egg.

During this development two moults occur, and after the second, the mother bites a hole in the silken cell and the brood escapes.

Twenty-four species of false-scorpions are known in Great Britain and rather less than a hundred in Europe. The order is split into two divisions, Panctenodactyli and Hemictenodactyli, based on the character of the chelicerae. Each division includes several families.

Harvesters

Unlike the false-scorpions, the harvesters, harvestmen, or harvest-spiders, which form the order Opiliones, are well known to all who are interested in Natural History. They are distributed over almost the whole of the world. But a curious feature of their distribution is that each family has a range in which it is greatly predominant and outside which its representatives are comparatively few. There are many different kinds, and species from tropical countries have sometimes a very remarkable appearance, unlike any of our native examples.

Despite one of their popular names, harvesters are very clearly distinguished from true spiders in having the abdomen and cephalothorax joined across their whole breadth, there being no waist or pedicle (Fig. 113). Further, the abdomen is clearly segmented, and there are no lung-books or spinnerets. In fact, the structure of a harvester more closely resembles that of some of the mites; but a clear distinction is to be found in the anal aperture, which is transverse or circular in harvesters, and always longitudinal in mites.

Although harvesters are never brightly coloured but always of varying shades of yellow and brown or black,

their bodies are beautifully sculptured and well worthy of examination. The cephalothorax bears two large eyes placed back to back on a tubercle so that they look sideways. This eye tubercle is usually decorated with spines, and the black eyes are sometimes surrounded by a white ring. The position and shape of the ocularium and the character of its spines are important features in classification. A group of spines is also situated in front of the eyes of many species.

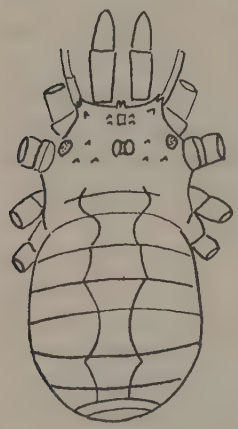


FIG. 113.—Body of a Harvester. After Pickard-Cambridge.

FIG. 114.—Chelicera of a Harvester.

The segments of the abdomen are marked by transverse rows of small tubercles. The abdomen has seldom any pattern, but a broad regular black band or vitta frequently marks the middle of the upper surface.

The appendages are the chelicerae, palpi, and legs.

The chelicerae are in no way striking. They are composed of three joints and are chelate (Fig. 114). The palpi are purely organs of touch. They have six joints and are leg-like in appearance, terminating in a single claw.

The legs are characterised by their great length and delicacy (Fig. 115). They have the same joints as the legs of spiders, but the tarsus has a number of rings or false articulations which give it an appearance different from any joint of a spider's leg. The legs of the first pair are always the shortest and those of the second pair are always the longest. Despite their clumsy appearance, the creature

is able to move with a fair turn of speed. The legs are very readily cast off if they are seized, and a harvester can only

FIG. 115.—Leg of a Harvester.

be caught by grasping two or three legs at once. The legs seem to be well endowed with tactile organs, like the legs of spiders, and in this respect must prove very valuable to the animal. A harvester may often be seen at rest on the trunk of a tree with its long legs spread out symmetrically round it, covering a large area. A slight touch on any part of one leg immediately causes the creature to drop to the ground.

The arrangement of the mouth parts of harvesters is very characteristic (Fig. 116). The mouth lies between an epistome in front and a labium behind, and is furnished at its sides with three pairs of maxillary lobes from the coxal joints of the palpi and the first and second legs. In a few species the second legs have no maxillae. Although the chelicerae are weak, the creature does not limit itself to liquid food as do spiders. Harvesters are essentially carnivorous and eat mites, centipedes, caterpillars, and spiders as well as each other. I have seen one carrying a butterfly in its jaws, but was not fortunate enough to see the capture, which must have been interesting. They do not scorn to eat the bodies of any of these creatures if they are already dead, but reject them if they are not fresh. They are thirsty animals and may often be seen drinking drops of dew when this is the

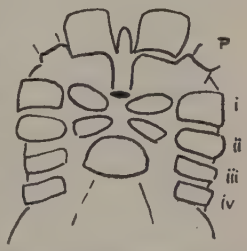


FIG. 116.—Mouth of a Harvester. P, Palp; i–iv, legs.

only available water. In extreme cases they obtain moisture from juicy plants.

It seems probable that the harvestmen are helped to escape from their enemies by giving out an odour. A pair of odoriferous glands lie in the forepart of the cephalothorax and their orifices are usually very conspicuous on the upper surface near the coxae of the second pair of legs. Simon compares the odour of the secretion produced by *Phalangium opilio* to the smell of walnuts, but it does not seem to be generally noticeable to our olfactory sense. So far I have never been able to detect it.

The sexes of harvesters do not as a rule differ much in external form. The males are usually smaller in the body and longer in the legs than the females, and their spines are often longer and more numerous. Sometimes they are more brightly coloured. They fight vigorously with each other during the breeding season. The sexual organs are ordinarily concealed, but if one gently squeezes the sides of a living harvester between finger and thumb the long ovipositor of the female or the intromittent organ of the male will be extruded. These are remarkable for their great length, which often exceeds that of the creature's body. In mating, the two harvesters stand face to face and the long penis of the male reaches forwards to the genital opening of the female. The female lays twenty or more eggs, in holes in the ground, under stones and under the bark of trees, unprotected by any cocoon. From the eggs there hatch out small but in most cases fully formed harvesters which have at first a uniform dull cream colour. At the first moult they acquire the normal markings. They moult five to nine times before reaching maturity. Only in a few cases is the mature harvester markedly different from the immature individual.

The Order, which should be called Opiliones and not Phalangidea, is divided into three sub-orders :

1. Cyphophthalmi.
2. Mecostethi or Laniatores.
3. Plagiostethi or Palpatores.

The first two sub-orders consist mainly of tropical species, and have no British and only a few European representatives.

Mites

Mites form an order of Arachnida which in numbers, in their economic importance, and in the complexity of their life-histories far surpass spiders, harvesters, and all the other orders. Their distribution is world-wide, for they extend from the arctic regions to at least the South Orkneys in the sub-antarctic ocean. Their diversity of habits is very great and their mode of life often remarkable in the extreme.

Mites are the smallest of the Arachnida, the majority of them being less than a millimetre long. The division between the cephalothorax and abdomen is marked by a transverse groove, but this is not visible in water-mites. The number of eyes is not constant, and many mites are blind. The appendages are the usual six pairs.

The chelicerae and palpi are subject to a great degree of modification in the different families. The former may be chelate or not, and sometimes they terminate in a single blade. In Ticks they form two long piercing weapons, with teeth on their outer edges. The palpi are scarcely noticeable in some forms. In the majority they are leg-like feeling organs and in the snout-mites are very long and antenniform. On the other hand, the palpi of some mites can seize their prey while the water-mites anchor themselves by their means. Maxillary plates are always developed from their coxae. The legs have six or seven joints, and end in one, two, or three claws, or in a sucking disk, or simply in a long bristle.

Owing to the great diversity of habits among mites and the correlated differences of structure it is most convenient to subdivide the order first and then to survey the groups in turn. The study of mites has progressed so rapidly in recent years that the earlier schemes of classification have been found to be inadequate, and agreement has not yet

been reached as to a trustworthy scheme. The arrangement adopted in this chapter is not intended to be more than a convenient one for the present purpose.

Nathan Banks, in 1915, divided the order of mites into eight groups called super-families, as follows :

1. Eupodoidea. Snout-mites.
2. Trombidoidea.
3. Hydrachnoidea. Water-mites.
4. Ixodoidea. Ticks.
5. Gamasoidea.
6. Oribatoidea. Beetle-mites.
7. Sarcoptoidea.
8. Demodicoidea.

The Eupodoidea are soft-skinned mites, generally found free-living in cold and damp places under moss, leaves, and decayed wood. One of the genera, *Linopodes* (Fig. 117), is characterised by the extraordinary length of its front legs, which are more than four times the length of its body. Clearly, such legs could not be used for walking ; they are held out in front as feelers. One family of this division is the Bdellidae, known as snout-mites on account of a prominent forwardly directed false head or capitulum.

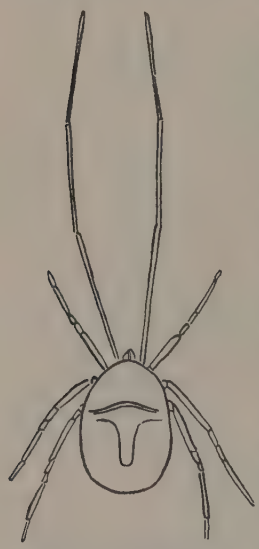


Fig. 117.—Linopodes, a Mite. After Soar.

The Trombidoidea are distinctly coloured mites which include the popular " red-spider," *Tetranychus telarius*. The Tetranychidae are also known as spinning-mites, for they have the power of producing silk from glands which open into the mouth and are probably modified salivary glands. Masses of vegetation are occasionally covered with their webs, under which the females lay their

eggs. These mites eat vegetable matter, and by sucking the sap of plants injure the leaves and give them a blistered appearance.

The most remarkable of the mites of this group belong to the family Cheyletinae. The normal members of this family have very large palpi, which are formidable weapons of attack. Unlike most mites they do not run or creep, but hop. A curious degenerate genus of the family is *Syringophilus*, which is parasitic in the interior of birds' feathers, where it is frequently to be found, and has a wide distribution. These mites enter the feather by the "superior umbilicus" (a minute slit at the junction of quill and vane) and live in the quill, feeding upon the pith until the feather is moulted or the bird dies. They then escape by the "inferior umbilicus" (a minute hole by which the pulp enters the base of the young feather) and seek a new host.

The "harvest-bugs" which often attack the hands and arms of labourers working in the fields belong to the genus Trombidium. The trouble is due to the larvae (perhaps of special species), which are particularly numerous in late summer and autumn. They attack any small mammal—rabbits, hares, and moles are frequent victims—forcing their mouth parts into the skin, which hardens round the pharynx in a cylinder, the so-called proboscis. The amount of trouble they cause varies greatly in different people. At its worst the skin swells and an intense irritation is set up. The natural scratching which follows often induces a rash, which may spread rapidly and be accompanied by a degree of fever. No disease, however, is known to be conveyed by these mites.

The Hydrachnoidea are aquatic mites consisting of two families. The Halacaridae are mostly marine mites, but some of them inhabit fresh water. They have hard bodies and a prominent capitulum, recalling that of the Bdellidae. Their legs are not adapted to swimming; they crawl upon the seaweed and burrow in the mud. The Hydracarina or fresh-water mites are when alive among the most beautiful

of all the mites, having a very rich and varied colouring. They also exhibit a great diversity of shape. Their legs are provided with long hairs and by their means the water-mites swim rapidly. They are predaceous, and their young stages are often parasitic upon other aquatic animals. They form a large group, with about two hundred and fifty species in Great Britain.

The Ixodoidea or Ticks are the largest of the mites. They are all parasites, which suck the blood of their hosts and thereby become enormously distended. When starved they are generally flattened in form. Their chelicerae are their cutting organs, with which they pierce the skin of their hosts, and behind the mouth there is always a hypostome set with backwardly directed teeth, which gives it an extremely firm hold of the skin into which it is thrust (Fig. 118).

Not many ticks are found in Britain, but from Africa and America come species which cause untold damage to cattle and crops. They have therefore been extensively studied.

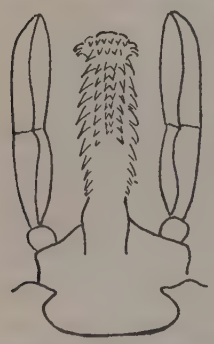


Fig. 118.—Chelicerae and hypostome of Ixodes.

The group consists of two families, Argasidae and Ixodidae. The former are parasitic on warm-blooded animals only and are responsible for the spreading of some rather uncommon maladies of men and animals in the Tropics. The trouble caused by ticks may be due to two reasons. Their bites may be irritating wounds, which extraneous bacteria on the foul-mouthed appendages may enter, producing sores and ulcers. More important, however, is the fact that parasitic within the tick there are often Protozoa capable of producing diseases in man and other animals. The very remarkable feature of these Protozoa is that they can remain alive in the body of the tick, even if the latter is unfed, for months or years. They may even be present in its eggs and in the larvae which

hatch from those eggs, so that the next generation of ticks is as dangerous as the first.

In the Argasidae, both sexes are capable of distension on feeding. The two most important genera of this family are *Argas* and *Ornithodorus*. A well-known species, *Argas persicus*, also known as the " teigne de miana " is a brownish Asiatic tick about five millimetres long. It is mainly a parasite of fowls, to which it conveys a disease called spirochaetosis. A similar disease of men in South Africa has been traced to *Ornithodorus moubata*, which contains the bacterium *Spirochaeta duttoni*. Another form, *Argas reflexus*, is a yellow and white tick, common near dovecotes and pigeon houses, which also attacks man. Its bite is very irritating, and at one time it was unpleasantly common in Canterbury Cathedral. The " Garapata " of Mexico, *Ornithodorus megnini*, attacks horses, oxen, and sometimes men about the ears ; *Ornithodorus turicata*, the " Turicata," is often fatal to poultry.

In the larger family, the Ixodidae, the whole of the back of the male is covered with a hard scutum and in consequence little distension is possible in this sex. In the female, the scutum forms only a small patch in front. The most familiar of all ticks is *Ixodes ricinus*, the common sheep-tick, specimens of which are often to be found on dogs if they have entered fields where sheep are pasturing. Fig. 119 was drawn from a tick collected in this way by the writer's springer.

The life-history of ticks is of great interest. The eggs, some thousands in number, are laid in a crack in the soil, where they hatch after an interval which varies from days to months and is dependent on the temperature. A larva emerges from each egg, like a small tick but possessing only six legs. These larvae climb the grass and wait in patient expectation until an animal brushes past. At the approach of an animal the young tick manifests great excitement, and, if possible, seizes its hair as it passes. Once secure, the larva plunges its rostrum into the skin and sucks the creature's blood until it is gorged. It then unhooks its

claws, withdraws its rostrum and drops to the ground again. Here it secretes itself in a crevice and rests while its huge meal is absorbed and other changes take place within. When these are complete, it casts its cuticle and becomes a nymph, with eight legs, but sexually immature. The nymph climbs the grass and repeats the actions of the larva. The moult which follows this second gorging produces a mature male or female tick which again seeks a host. Fertilisation takes place on the third host, the female being often the active member of the pair during

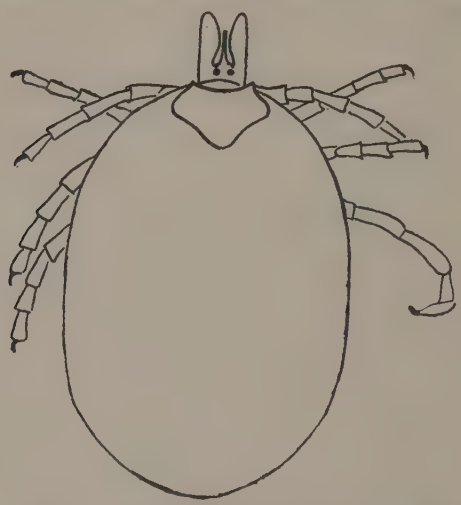


FIG. 119.—Ixodes ricinus. The sheep tick.

mating. Finally, the well-fed and fertilised female drops to the ground again and lays her eggs.

Although in some species of ticks, all the changes from larva to adult may be passed through without leaving the first host, it is a more general rule that three hosts are visited. It is a remarkable feature of ticks that they are well adapted to this extraordinary life-history, for they are able to undergo prolonged fasts without dying, and they seldom let slip a chance of attacking a host. Yet thousands must perish before an animal comes into their neighbour-

hood; as Shipley remarks, "it is terrible to think of the amount of unsatisfied desire which must be going on in the tick world."

At least one genus of ticks, *Aponoma*, confines its attention to reptiles and is therefore of little economic importance, but nearly all the other genera include species known or suspected to be transmitters of disease. The following are a few of the more important diseases propagated by ticks:

1. Texas fever or redwater, in cattle, by *Boophilus* spp.
2. Rhodesian fever, in cattle, by *Rhipicephalus appendiculatus*.
3. Carceag, in sheep, by *Phipicephalus bursa*.
4. Heartwater, in sheep and goats, by *Amblyomma hebraeum*.
5. Canine piroplasmosis, by *Rhipicephalus sanguineus* and by *Haemaphysalis leachi*.

The Gamasoidea, also known as the Parasitoidea, form a numerically large group, whose British species have not yet been fully studied. They are pale-coloured carnivorous mites, both free-living and parasitic. The mites which are found as parasites on bats belong to this group (Fig. 120), and so do the mites often found attached to beetles and other insects. One genus, *Halarachne*, lives in the bronchial passage of seals, and another, *Pneumonyssus*, in the lungs of old-world monkeys—good instances of the extraordinary haunts chosen by mites. The members of the sub-family Dermanyssinae are found on poultry and cage-birds.

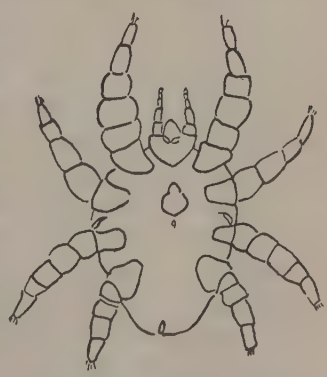


FIG. 120.—Spincturnix sp. from a bat. Partly after Soar.

The curious beetle parasites, of the sub-family Uropo-

dinae, are attached to their hosts solely for transport, and not as true parasites. They are fixed by a thread, which the mite can sever at will, and which consists of consolidated excrement.

The Oribatoidea owe their popular name of beetle-mites to their hard cuticle. They are all blind, all under a millimetre long, and are free-living. They are vegetable feeders and are found in dead wood, under bark, and amongst moss or lichen. Although blind, they are sensitive to bright light and always move away from it. Many of them have the curious habit of collecting dust and dirt on their backs, and this quite masks their true shape.

The Sarcoptoidea form a numerous group of mites, some of which are familiar. The typical genus, *Sarcoptes*, includes *Sarcoptes scabiei*, which is popularly known as the itch-mite. These mites are only a little longer than broad and look like extremely diminutive pearly-grey tortoises, with four legs directed forwards and four backwards. Their cuticle is translucent and is strengthened by transverse folds, which also occur on the legs. The legs end in suckers or hairs. The male and female meet on the skin of the host and after pairing the male dies. The female begins to burrow in the skin laying eggs behind her as she goes, and may continue this for two or three months, by which time she has laid about a hundred eggs. She cannot retreat from this burrow because of the spines with which her body is covered, and she cannot turn round in it, for it is too narrow. Thus she digs her own grave. The eggs hatch within a week and are mature within a month, so that infection soon spreads upon the body of the host. The mature mites, when seeking each other on the surface, may be transferred by contact to other persons or to horses, cattle, dogs, cats, and even camels and lions.

Another species, *Sarcoptes mutans*, causes the "leg scab" of poultry.

The smooth soft-bodied mites of the family Tyroglyphidae, also belong to this group. They include *Tyroglyphus siro* and *Tyroglyphus longior*, which are the

familiar cheese mites. Some of them are very destructive to stored roots and bulbs.

The smallest of all known mites are also members of the same group. The best-known example is *Acarapis* or *Tarsonemus woodi*, which lives in large numbers in the tracheal tubes of the honey bee, and causes " Isle of Wight disease."

The Demodicoidea include two families, of which the first contains but one genus, *Demodex*. These are microscopic skin parasites, living in the hair follicles of mammals. They are the cause of follicular mange. A common species, *Demodex folliculorum*, infests the skin of man and is so widespread that Guiart says " nous en sommes presque tous porteurs." They are in themselves quite harmless.

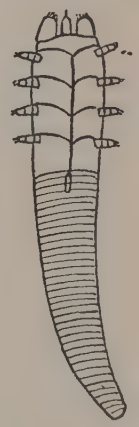


FIG. 121.—Demodex. From a dog.

All these " worm-like " mites have a very long annulated abdomen (Fig. 121). The other family of the group, Eriophyidae or Phytoptidae, are known as gall mites and are vegetable feeders only. They are unique in possessing only two pairs of legs, and are the cause of some of the curious growths which occur on the leaves and buds of plants. Sometimes they do no great damage, but at least one of them, *Eriophyes ribis*, which feeds on the buds of the black currant, has been a serious pest to fruit-growers.

Mites make a good conclusion to a book on Arachnida because they remind us once more of the varied forms that Life may take. Within the limits of a single Class we find a wide diversity of habit and a remarkable choice of haunt, emphasising better than anything else the intensity of the struggle for existence. To this struggle many of the phenomena of biology may be traced.

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